THE EFFECTS OF AGRICULTURAL LAND-USE ON THE BREEDING ECOLOGY OF LAPWINGS *VANELLUS VANELLUS*

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DECLARATION

I declare that this thesis, composed by myself, has not been accepted in any previous application for a degree. All sources of reference and quotation have been duly acknowledged

CONTENTS

ABSTRACT

The primary aim of this project was to investigate the relationships between agricultural land-use and the breeding ecology of Lapwings by comparing breeding biologies in two different habitats - arable farmland and rough grazing. Both land-use policy and specific farming operations have important effects on all aspects of Lapwing breeding biology, including nesting habitat choice, timing of laying, clutch and egg sizes, hatching and fledging success.

In the first two years of the study, productivity on the arable site was too low to maintain the population. This was due to a combination of timing of farming operations, crop growth and habitat availability. In the final year, poor weather in the early spring disrupted cultivation and retarded crop growth and breeding success on the arable site was comparatively high. In all three years productivity on the rough grazing site was sufficient to maintain the population (in spite of a higher level of predation). The difference between the two sites was due to their markedly different land-use policies.

A secondary aim of the project was to investigate the possibility of behavioural limitation of breeding density and success in Lapwings. Lapwings on the rough grazing site apparently compete for high quality habitats which they occupy preferentially and within which breeding success and nesting density is high. Lower quality habitats, in which breeding success and population density is reduced, are filled later. These results conform to the predictions of the ideal despotic model and suggest that a mechanism exists whereby behavioural limitation might take place.

The conservation and population dynamics implications of these findings are discussed.

Chapter 1. GENERAL INTRODUCTION

The ecological relevance of studies of breeding waders

Ecologists have directed a great deal of attention toward identifying the factors affecting animal distributions and population dynamics. Much of this work has concentrated on birds. The reasons for this are partly historical: the upsurge in interest arose from the publication of seminal works which, since their authors were primarily ornithologists, relied heavily on previous avian studies (Lack 1954 and 1966, Wynne-Edwards 1962). However, the trend is also attributable to the relative ease with which many species of birds can be studied.

Studies of the processes which might influence the distribution and abundance of waders (Charadriidae), have mainly been carried out during the non-breeding season. At this time the birds may be concentrated in habitats (usually marine or estuarine shores) where, because of the open topography, their survival, social interactions, feeding behaviour and diets can be studied easily. During the breeding season, however, waders become more secretive and are generally well dispersed in habitats which are less open or accessible. Because of the methodological difficulties that these changes in behaviour and habitat pose, comprehensive breeding studies of waders are few. Nevertheless, without such research our understanding of the factors affecting wader population dynamics will be incomplete and the relationships which have been shown to exist during the non-breeding season cannot be placed in context.

At present, too few studies have been carried out to draw any general conclusions regarding the importance of breeding season factors in the regulation of wader populations. However, some which do exist suggest that population regulation may be effected through territorial behaviour on the breeding grounds (Harris 1970, Holmes

1970), although this interpretation and the general relevance of these studies has been questioned (Evans and Pienkowski 1984). Only further carefully planned field studies will shed light on these problems.

Why farmland waders?

The effects of anthropogenic factors on avian population dynamics have received comparatively little attention. In Britain, however, such factors are likely to be of great importance for certain wader species, since some form of agricultural land is their usual nesting habitat (Galbraith and Furness 1983, Galbraith et al. 1984).

As well as being of considerable academic interest, studies of the effects of agriculture on avian population processes may have important conservation implications. During the last 40 years farming in Britain has changed fundamentally. The traditional mixed farming system, with its diversity of crops and mix of cultivation and livestock rearing, has, in many areas, been replaced by larger-scale units (formed through the amalgamation of smaller farms) specialising in particular crops, especially cereals. Even in upland areas where, because of unfavourable topography, climate or soil type, cereal cultivation is not economically viable, widespread changes have occurred due to the drainage and improvement of hitherto marginal grazing land. These trends toward cerealisation on lowland farms and land improvement in upland areas have been generated by both technological advances, and by various direct and indirect subsidy systems provided by the government and, more recently, through the Common Agricultural Policy of the European Economic Community.

Our knowledge of the possible effects that these agricultural changes might have on animal populations is inadequate. Although drastic effects, such as those due to the overuse of pesticides, have been well documented, the more subtle effects which are likely to

follow from habitat modification are less easy to detect and largely unknown. There have, however, been reports of reductions in local breeding populations of waders following changes in agricultural land-use (Green 1980, O'Connor and Shrubb in press.). If effective conservation policies are to be formulated, more information is required on the ways in which particular farming practices and policies may modify the population processes of wild animal populations on farmland.

Why lapwings?

Lapwings Vanellus vanellus are suitable animals with which to investigate the inter-relationships between agriculture, population biology and conservation for three main reasons: firstly, they are fairly abundant and widely distributed throughout British farmland. During the survey for "The Atlas of Breeding Birds in Britain and Ireland", Lapwings were confirmed as breeding in approximately 73% of the British and Irish 10km squares (Sharrock 1976). Secondly, Lapwings occur in fairly high breeding densities (to the extent of appearing semi-colonial in some areas), which facilitates the collection of data. Lastly, while they are characteristically birds of farmland, they breed in a variety of habitats within that broad classification (Nicholson 1938, Lister 1964, Galbraith and Furness 1983, Galbraith et al. 1984). The two Scottish agricultural habitats in which the highest densities occur are rough grazing (i.e upland marginal grass-land) and lowland arable land, especially cereal fields (Galbraith et al. 1984). As already noted, these are the two habitats most affected by current agricultural changes. By comparing breeding ecology and productivity in both habitats, this study investigates the role of agricultural influences on Lapwing population processes and the resulting conservation implications.

The general biology of Lapwings

Throughout their breeding range, Lapwings are birds of open treeless country and their ancestral habitat was probably the steppes of eastern Europe and the Middle East. The expansion of farming into Europe is likely to have created much new breeding habitat, as the woodlands, which constituted the climax vegetation, were replaced with open fields.

Lapwings are mainly summer visitors to their breeding areas, arriving between February and April and leaving in late-summer. Non-breeding season movements are, to a great extent, weather dependent: Lapwings from northern Britain move only short distances except during severe weather when they move south and west into Eire, France and Iberia (Imboden 1974). If they are unable to escape severe winter weather, large-scale mortalities may occur. During the non-breeding season the birds inhabit mainly open country such as estuaries and high quality farmland where there is a rich invertebrate food supply.

Soon after their arrival in the breeding area, male Lapwings become very territorial and establish their claims to territories through spectacular song flights and aggressive ground displays (Cramp and Simmons 1983). Females are not usually territorial. Birds may breed for the first time when one year old, however, the actual proportions breeding at this and subsequent ages are unknown (Kraak et al. 1940).

In most Lapwing populations which have been closely studied a proportion of males have been polygynous (e.g Rinkel 1940, Laven 1941, Elliot 1982). Without individually colour marking all of the birds in the population, it is difficult to estimate the extent of polygyny, but during the present study it appeared that polygyny occurred in a minority of males, with bigamy being the most common form and trigamy less usual.

In common with most other waders, Lapwings are ground-nesters and the usual clutch is of four eggs (Cramp and Simmons 1983). If a clutch is lost, for example through predation, the female can relay and can repeat this operation for up to four or five clutches if necessary (having done so a female has produced approximately twice her own weight in eggs). The interval between losing one clutch and beginning another may be as short as five or six days (Klomp 1951). Most of the incubation is carried out by the female, with the male standing guard against predators. Both adults mob potential predators vigorously. The incubation period is approximately 25 days and the fledging period about 35 days. During the first 10 days after hatching the female broods the chicks at frequent intervals, but with decreasing frequency thereafter (Cramp and Simmons 1983).

Apart from depending on the parents for defence against predators and brooding, the chicks are entirely independent. Within a few hours of hatching they are able to run about and feed themselves. The first-hatched chicks will, however, remain in the nest cup until all of their siblings have hatched and are ready to go (Spencer 1953).

Once fledged, the juveniles either leave their natal area or join flocks composed of other juveniles and adults, which have either bred successfully or are failed breeders (many of the adults are in moult by this time). These flock birds normally vacate the breeding areas by early August.

Thesis structure

The remainder of this thesis is in seven sections: Chapter 2 is a description of the two study areas in terms of their vegetation, topography and agricultural land-use, and also outlines the general study methods used. Chapters 3 to 6 describe the effects of environmental influences during the course of the breeding season from

first arrival and nesting habitat selection (Chapter 3), through laying (Chapter 4), hatching and fledging success (Chapter 5), and chick diet and movements in relation to food availability (Chapter 6). Throughout these four chapters particular emphasis is placed on the effects of land-use patterns. In Chapter 7 the relationships between social behaviour, habitat quality and breeding dispersion and success are described and the possibility of population limitation through social behaviour discussed. Chapter 8 comprises a general discussion of the results of the study in which the population and conservation implications are considered.

Chapter 2. STUDY AREAS AND GENERAL METHODS

2.1 STUDY AREAS

The two study areas were located in the Midland Valley of Central Scotland (Fig. 2.1) and, although only eight miles apart, they differed widely in topography and land use, and, because of their different altitudes, to some extent in climate.

2.1.1 The arable site

The arable study area lay at sea level on the Carse of Stirling (Stirlingshire/Perthshire = Central Region) and comprised 9.01 km^2 of flat, comparatively well drained and intensively cultivated farmland on which the main crops were cereals, grass (mainly for hay with smaller quantities for silage), beef and mutton (Table 2.1). The crop areas in Table 2.1 were obtained by plotting field boundaries on a 1:10000 scale map and measuring field areas using a Summagraphics Digitiser linked to a microcomputer. Repeat measurements on a small, medium and large field showed that the accuracy of this method varied with field size: the means of 10 measurements on each field were 1.5, 3.9 and 9.6ha and the mean error for each set of measurements (as a percentage of the mean area) was 4.2, 1.8 and 1.0%, respectively. These levels of accuracy are considered adequate for medium and large-sized fields. However, to reduce the error in the measurement of small field areas, fields of less than 3.0ha were measured four times and the mean value taken.

Table 2.1. Land use on the arable site during the study period. "Other" includes farm buildings, roads etc.

CROP	1984 AREA(ha)	(%)	1985 AREA(ha)	(%)	1986 AREA(ha)	(%)
SPRING OATS	215	23.8	225	24.9	287	31.8
SPRING BARLEY	92	10.2	69	7.5	70	7.5
WINTER WHEAT	47	5.2	41	4.5	41	4.5
WINTER BARLEY	11	1.2	0	0.0	0	0.0
HAY/SILAGE	293	32.5	312	34.4	273	30.3
PASTURE	174	19.3	171	19.0	171	18.9
OILSEED RAPE	17	1.9	29	3.2	0	0.0
PEAS	6	0.7	8	0.8	14	1.5
ROOT CROPS	1	0.1	1	0.1	0	0.0
OTHER	45	5.0	45	5.0	45	5.0

The mixture of crops in Table 2.1 is typical of lowland Scottish farming except that barley, not oats, is usually the main cereal crop (during the five years from 1979 until 1983 the acreage of barley exceeded that of oats in Scotland by a factor of 13 (Department of Agriculture and Fisheries for Scotland 1979-1983)). The emphasis on oats in the study area is partly traditional and partly attributable to the tolerance of oats to the high clay content in the soil. Barley is a less suitable crop for this area since it requires a lighter soil.

The nature and timing of farming operations varied from field to field depending on weather and the crop. Fields in which spring cereals are to be grown are ploughed in the autumn then left undisturbed until the following March or early April when they are given an application of powdered nitrate and/or phosphate, sown and then rolled within a few days of sowing. In wet years when the soil

may be water-logged (such as 1986), cultivation may be delayed by 2 - 3 weeks. After rolling, the spring cereal fields are not disturbed until mid-May when chemical control agents may be applied. During the study period, pesticides were used sparingly on spring cereals and the only treatment for most fields was one application of herbicide. Fields used for winter cereals were ploughed and sown in the autumn then left undisturbed until herbicide, fungicide and insecticide were applied (where necessary) in May.

From my own casual observations it is clear that spring cereal emergence takes place in early May in normal years, and by mid-May the crop is 10cm high, growing to 50cm by mid-June. Winter cereals emerge in the autumn of sowing and by winter, when growth stops, have reached a height of 10cm. Growth is resumed the following spring and for the rest of the growing period winter cereals are consistently 10 - 15cm taller than spring cereals. Crop germination and growth may be retarded by low temperatures and high rainfall (as happened in 1986 when, due to water-logging and low temperatures in April and May, growth was retarded by about four weeks and germination was patchy in many fields).

In hay fields, late-summer mowing reduces the grass to a short stubble which persists throughout the following winter until growth resumes in April. By mid-May the hay crop is 20cm high, growing to approximately 50cm by early June. The first cut of grass for silage takes place in June and the first hay is mown in July.

Except for the activities of grazing animals, most pasture is undisturbed throughout the year. The average grass height in the pasture fields varies between about 3 and 20cm depending on the density and species of grazing animals: high stock densities result in a short sward and sheep tend to graze the vegetation shorter than cattle.

Apart from permanent pasture, the fields on the arable site had traditionally been subject to a four year rotation, i.e three years as hay then one year under cereals and back to hay in the following year. However, the use of chemical fertilisers and the availability of pest control agents, together with a reduced demand for hay and the financial inducements offered for cereal production, have resulted in most fields being sown with cereals for much longer periods (up to 12 years in succession). This change has been most marked on the larger farms where specialisation on cereals is more profitable. On some of the smaller farms the traditional rotation still survives.

2.1.2 The rough grazing site

The rough grazing study area was located in approximately 8 km^2 of largely unimproved, poorly drained hill farmland at 150m above sea level near Fintry, Stirlingshire (Fig. 2.1). Most of the area is only partly enclosed and provides grazing for small numbers of beef cattle and sheep. Except for scattered conifer plantations, no other crop is grown. For the most part, the vegetation is dominated by coarse grasses (mainly Deschampsia flexuosa, Nardus stricta and Mollinia caerulea), Moor Rush Juncus squarrosus and stunted Heather Calluna vulgaris. In the wetter areas, Juncus spp., Cotton Grass Eriophorum vaginatum, Deer Sedge Scirpus caespitosus and sphagnum mosses predominate. In places, an attempt has been made to improve the quality of the land by the application of lime and these areas contrast visually with the surrounding unimproved land due to the dominance of greener, lusher grasses (particularly Festuca ovina and Agrostis tenuis), together with a greater abundance of herbs and legumes such as Potentilla erecta and Trifolium repens. More or less widely spaced Juncus clumps are dotted about these improved areas.

Throughout the rough grazing study area the vegetation is kept short by grazing, particularly in the improved areas where cattle and sheep concentrate and where the mean grass height is approximately 5cm. On the unimproved areas the grass height in June and July reaches about 10 - 15cm.

2.1.3 Climate in the study areas

Although few measurements were made, it was apparent that, due to the greater altitude, the rough grazing site was generally cooler, wetter and windier than the arable site. On 10 occasions between February and May, the temperature at 15cm above ground level was recorded at both sites (with an elapsed time of less than 30 minutes between observations). On average, the rough grazing study area was 2.1^{o}C cooler than the arable site. Daily weather records appropriate for the arable site were obtained from Stirling University Weather Centre which is located three miles away and at a similar altitude. 1984 and 1985 were similar in their weather patterns during the study periods, but in 1986 the weather was cooler in April and wetter in May (Fig. 2.2).

2.2 GENERAL METHODS

In each subsequent chapter, methods specific to that aspect of the study are described as relevant. Here I shall outline the general methods used for all aspects of the study.

2.2.1 Nest finding and marking

Most nests were found by locating incubating adults either from a vehicle or a hide. Since adults normally visit the nest only briefly during laying, comparatively few nests were found prior to clutch completion. To aid subsequent observations, each nest position was marked with short lengths of garden cane stuck upright in the ground

between 20 and 30m from the actual nest site. The possibility that marking might increase the risk of predation by giving predators a clue to the whereabouts of the nest (Picozzi 1975) was investigated in 1985 in an area peripheral to the arable site: just after laying had begun 32 nests were found in spring cereal and hay fields. 17 were marked and 15 left unmarked but their positions fixed by recording the distance and compass bearing from the nearest obvious landmark (where there were no landmarks a cane was stuck into the ground 75m from the nest to provide a reference point). Two weeks after marking the last nest, the area was re-visited and the fate of each nest checked. 12 of the marked nests still contained their original clutches, one had lost an egg and four were empty. 10 of the unmarked nests were intact, four were empty and one could not be found and was presumed predated. Although the controls actually suffered a slightly higher predation, the difference between the two groups is not significant (X^2 = 0.260, 1df, p>0.50), indicating that nest marking, as practiced, did not affect the likelihood of clutch predation.

2.2.2 Egg measurements

If a nest contained the normal clutch size of four eggs when found, the length and breadth of each egg was measured to the nearest 0.1mm using vernier calipers, and it was weighed to the nearest 0.1g using a Pesola or Salter spring balance. If fewer than four eggs were in the nest it was re-visited a few days later (when the clutch should have been complete), the clutch size recorded and the eggs measured and weighed.

An estimate of egg volume can be obtained from $L \times B^2 \times K_v$, where L = length, B = breadth and K_v = a volume constant (Hoyt 1979). K_v is a function of egg shape and more rounded eggs have a higher value than eggs which are pyriform (such as the eggs of most

Charadriids). K_v was estimated for Lapwing eggs by filling 30 from the Glasgow Museum egg collection with measured quantities of water. A regression of volume against LB^2 gave the equation: $V = 0.425LB^2 + 1.678$. The correlation coefficient was 0.963 indicating that at least 93% of the variation in egg volume could be explained by length and breadth differences alone. K_v was calculated by dividing the measured volume of each egg by its LB^2, giving a mean of 0.457 (s.d = 0.013). This value of K_v differs from that which would be obtained by water displacement since the latter includes shell volume. The index given in this study gives internal volume of the egg. The reason for using water filling rather than displacement was that the former gives a much more precise measure (since the quantity of water injected using a hypodermic syringe can be measured more accurately than that displaced in large graduated cylinders).

This value of K_v was used to estimate the volume of each egg found and the mean egg volume in each clutch.

2.2.3 Catching, marking and measuring adults

If wader fledging success is to be investigated, it is essential that individual study broods can be identified (preferably from a distance so that disturbance is kept to a minimum). The most reliable method of identifying broods is to individually mark the parents. Some adult Lapwings were individually recognisable by virtue of soft parts or plumage characteristics such as lameness (many have deformed legs or feet, probably through having wool caught on them as chicks), lack of crests, or differences in their face patterns. Individually recognisable adults were too few, however, to constitute adequate sample sizes and it was necessary to artificially mark breeding birds. Several marking methods were used:

a) in the year before the study began some chicks in the rough grazing

study area were given unique combinations of Darvic colour rings and a few of these were present as breeding adults during the first year of the study. Intensive chick ringing during the following two years resulted in yet more birds marked by this method returning as breeding adults.

b) nest-trapping and marking of breeding adults. Walk-in traps and clap nets, have been shown to be effective and safe for catching breeding adults of some other wader species e.g, Oystercatchers Haematopus ostralegus (Harris 1967), Dunlin Calidris alpina (Soikelli 1967) and Golden Plovers Pluvialis apricaria (Parr 1979). Lapwings, however, are extremely wary birds and refused to return to nests over which walk-in traps had been placed. An elastic-powered clap net was effective in catching adults on their nests but resulted in desertion at four out of 20 nests where this was done. Because of this high desertion rate, clap-netting was discontinued as a catching method in the study areas (although it was used to obtain biometrics from some incubating adults elsewhere).

c) the easiest and least intrusive method was found to be remote marking using nest "sponges": small wads of cotton wool soaked in a saturated solution of picric acid in water were placed in plastic culture dishes, 1cm deep and 3.5cm wide, in shallow depressions on the rim of the nest cup. The culture dishes prevented the dye from draining away and the cotton wool from drying out. When the adults sat on the nest, the sponge pressed against their white breast feathers dyeing them bright yellow. In many cases adults refused to sit on sponges which were too obvious, however, they returned to the nest and quickly resumed incubation if the sponge was camouflaged in some way. It was found that the simplest method was to cover it in a thin layer of dried sphagnum moss. When the bird resumed incubation its breast pressed the moss down against the sponge and the moss

wicked up the dye and transferred it on to parts of the breast feathers.

At frequent intervals, incubating adults change position slightly, with the result that the dye was spread over a large area of the breast feathers. Incubating adults normally face into the wind so an appropriate position for the nest sponge could be judged from wind direction. On windless days the orientation of the adult relative to the nest cup was noted before disturbing them, and the sponge placed accordingly.

Nest sponging resulted in a conspicuous yellow breast patch which was easily visible (using 10x binoculars) at distances in excess of 100m. Moreover, because of chance differences in the position and intensity of the dye and deliberate placing of nest sponges in relation to the expected incubation orientation of individual birds, most adults were, effectively, individually marked.

Since picric acid is a permanent dye and is lost only when the birds moult the dye-marked feathers in the autumn, birds marked by nest sponging retained their dye throughout the breeding season. The main disadvantage of this method of marking, however, was that the birds had to be marked anew each year, but by using several sponges simultaneously, a comparatively large number of birds could be marked quickly.

Using a combination of these techniques (with most emphasis during the last two years of the study on nest sponging), sufficient numbers of adults were individually marked to allow the nesting success of individual pairs to be investigated (Table 2.2).

Table 2.2. Numbers of individually marked breeding adult Lapwings available during the three years of the study. "Plumage characteristics" comprises both feather patterns and soft part characteristics e.g lameness.

	PLUMAGE CHARACTERISTICS	COLOUR RINGED	NEST SPONGED
1984	10	4	7
1985	7	15	21
1986	5	20	25

All adults caught had several body measurements recorded: wing length (maximum chord), bill length (tip to feathering), head and bill length, tarsus length, foot length and weight. Wing and foot length were measured to the nearest 1mm using a 300mm stopped rule. Foot length was obtained by pressing the leg flat against the rule with the heel against the stop, and measuring to the end of the longest toe (excluding the claw). Bill, head and bill, and tarsus length were measured to the nearest 0.1mm using vernier calipers and weight was taken to the nearest whole gram on a Pesola or Salter balance.

2.2.4 Chick marking and measuring

Chicks were marked with numbered British Trust for Ornithology metal rings and, in those broods used in the investigation of fledging success, also with temporary PVC leg flags (Goodyer et al. 1979), in brood specific colours. Leg flags were recognisable through a 45x telescope at distances of up to 100m and were used, in conjunction with adult marks, to identify study broods without the disturbance that a close approach would cause. Goodyer et al. (1979) reported loss of leg flags among adult waders wintering on the Tees Estuary, England. This was not a problem in this study however, since none of the hundreds of chicks which were metal ringed, leg flagged and subsequently recaptured had lost their leg flags. Once chicks reached

about three weeks old, they were given unique combinations of Darvic colour rings which identified them if they returned in subsequent years.

Chicks were weighed using Pesola and Salter spring balances (to 0.1g), and their head and bill, bill, ninth primary and tarsus lengths measured to 0.1mm using vernier calipers. Wing and foot lengths were measured to the nearest 1.0mm on a stopped 300mm rule. To avoid unnecessary disturbance, biometrics were not collected from broods in which chick movements and survival were being studied.

2.2.5 Invertebrate sampling

Different methods were used to sample surface living and sub-surface living invertebrates:

a) sub-surface. Using a garden spade, soil samples $20cm^2$ and 10cm deep were collected from all of the major study habitats (improved and unimproved rough grazing, spring and winter cereals, hay and pasture fields). Digging was found to be an easier, quicker and more reliable method of sampling mobile invertebrates than using a soil corer (each sample took less than 20 seconds to collect), thus reducing the amount of time available for animals to escape by burrowing into deeper layers. Each sample was placed in a plastic bag, taken to the laboratory and hand-sorted within 24 hours of collection.

The efficiency of hand-sorting in providing absolute population estimates of earthworms varies between species and soil types (Raw 1960, Nelson and Satchell 1962, Edwards and Lofty 1972). Smaller and darker animals tend to be missed and the method is less efficient in heavier soils. Nevertheless, for the comparative purposes of this study and, given the major differences in earthworm numbers between habitats, the accuracy of the hand-sorting method was considered adequate.

The invertebrates from each sample were sorted into three groups: earthworms, leatherjackets and others (mainly beetles and their larvae), and oven-dried at 60°C to a constant weight.

b) surface. Surface invertebrates were sampled using pitfall traps. These consisted of plastic beakers (circular in cross-section, 8.5cm deep and 7.0cm in neck diameter) containing a small quantity of 5.0% formalin solution as a preservative and buried up to their rims in the soil. The insects caught were identified (usually to a Family level), and they were oven-dried at 60°C to a constant weight.

Southwood (1978) has summarised the known sources of bias when pitfall traps are used to provide relative population estimates. These include weather and general habitat differences in the area surrounding the trap (Mitchell 1963), the type of preservative used (Luff 1968, Greenslade and Greenslade 1971), time since placement (Greenslade 1973) and trap design (Luff 1975). In this study, pitfall trapping was used only to compare broadly similar habitats. Trap design, preservative and time since placement were constant between habitats and all traps were in operation simultaneously and so exposed to the same weather conditions.

Initially, surface invertebrates were also sampled using a "D-VAC" suction trap equipped with a single stroke petrol engine and a 10cm diameter nozzle. However, suction trapping sampled mainly smaller invertebrates living on plant stems and leaves and not the larger ground-living taxa (such as Coleoptera) on which Lapwings were found to feed (Chapter 6). Suction trapping was, therefore, discontinued as a sampling method.

2.2.6 Statistical procedures

All information was stored on the Glasgow University ICL2988 computer and the analyses carried out using SPSS programmes (Nie et al. 1975).

Differences between variances were checked for significance using variance ratio tests (Sokal and Rohlf 1969) prior to parametric tests being used. Where variances were significantly different, the data were either transformed or non-parametric tests were used (Siegel 1956). Non-parametric tests were used on much of the behavioural data since it was unlikely to conform to assumptions of normality. All regression analyses were carried out using the method of least squares.

Figure 2.1

Location of the two study areas. "A" is the arable site and "B" the rough grazing site. Contours are in feet.

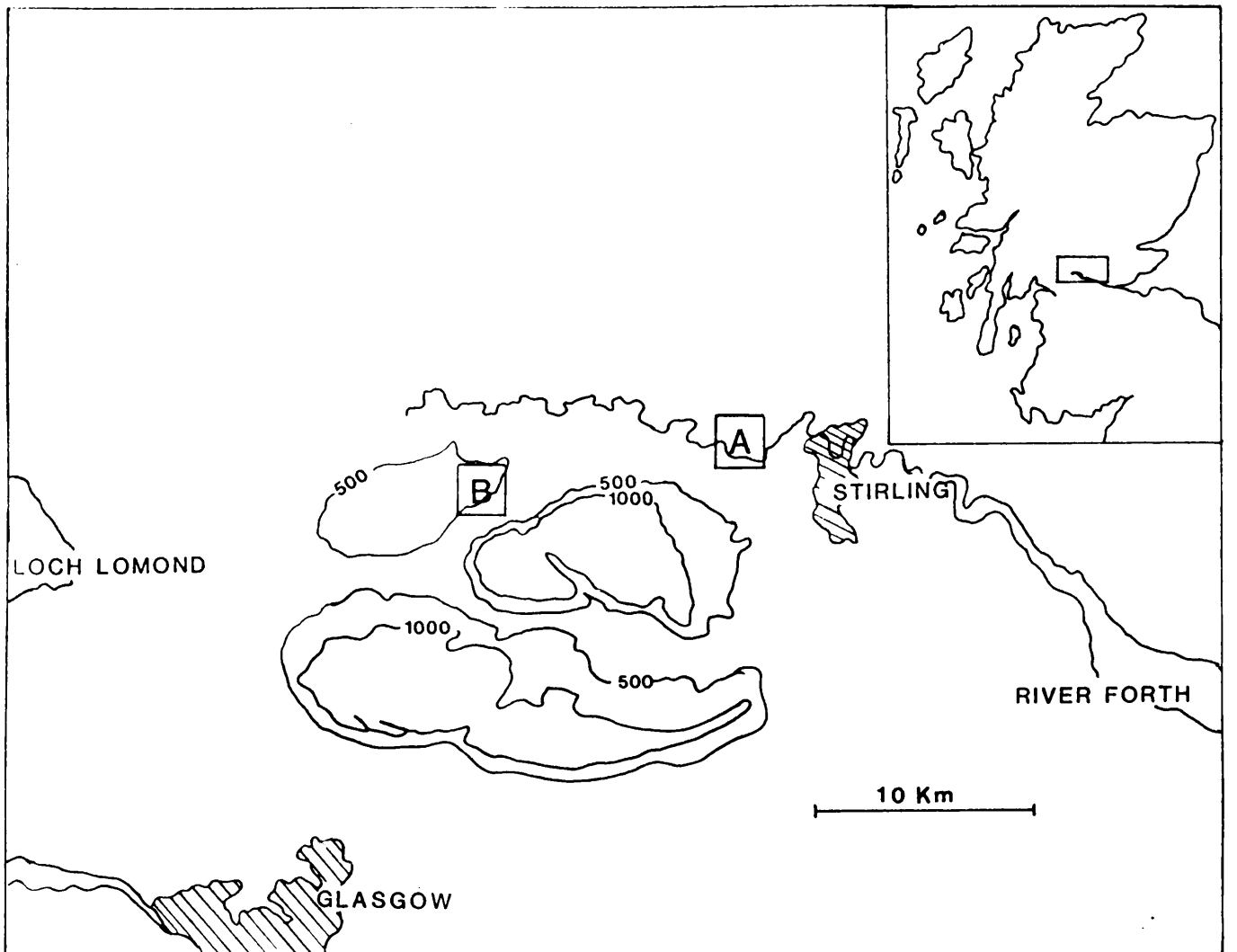
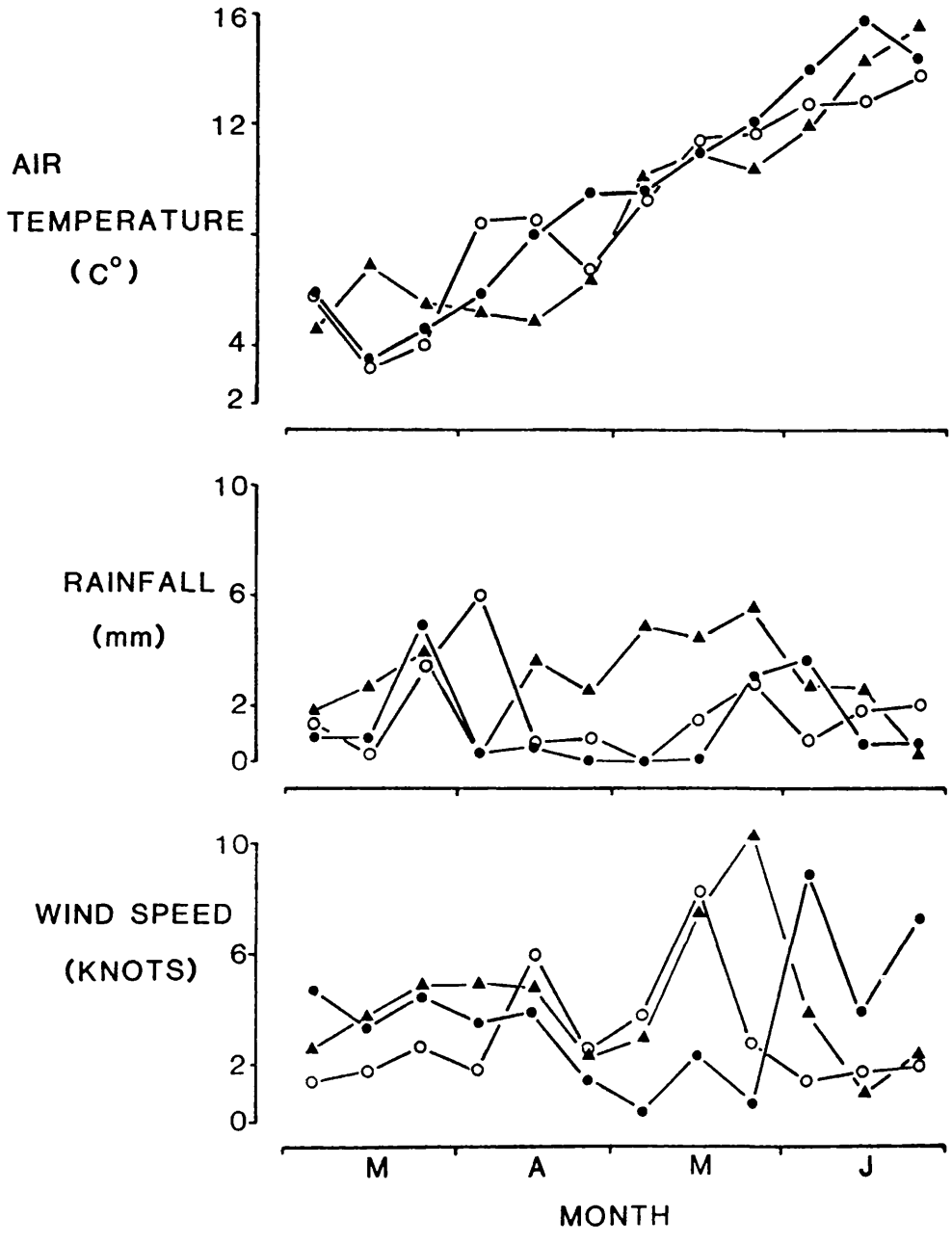

A
B
500
500
1000
1000
500
LOCH LOMOND
STIRLING
RIVER FORTH
10 Km
GLASGOW

Figure 2.2

Weather records from Stirling University during the three years of the study. Closed circles = 1984; open circles = 1985; triangles = 1986.


AIR
TEMPERATURE
(C°)
16
12
4
2
RAINFALL
(mm)
10
6
2
0
WIND SPEED
(KNOTS)
10
6
2
0
M
A
M
J
MONTH

Chapter 3. THE PRE-LAYING PERIOD - ARRIVAL, TERRITORY OCCUPATION AND HABITAT UTILISATION

3.1 INTRODUCTION

Hilden (1965) identified three factors which are likely to be important in the selection of avian breeding habitats: food availability, protection from predation and constraints imposed by the morphological characteristics of the species. In common with other members of the Charadriidae, Lapwings have comparatively short legs and are morphologically adapted to exploit open habitats with short vegetation. The role of food and predation in the selection of breeding habitats is, however, not so obvious.

Whereas the diets and feeding behaviour of waders on their winter areas have been well studied (e.g various authors in Evans et al. 1984) little is known about these factors during the breeding season - a time of high energy demand (Drent and Daan 1980). The breeding habitat must supply enough food for the adults during territory occupation, egg laying and incubation, and must also cater for the population increase brought about by the chicks hatching. Thus the selection of breeding habitat is likely to be closely linked in some way with food availability.

Being ground nesting birds, predation levels on the clutches and chicks of waders are generally high (Chapter 5). This has resulted in the evolution of distraction and mobbing behaviour and cryptic eggs, chicks and adults. However, the efficiency of these adaptations depends on the correct choice of an appropriate breeding habitat. Thus, Elliot (1982) showed that Lapwings were effective in excluding avian predators from their nesting areas by mobbing, but they tended to nest only in areas where there were few or no trees from which crows could operate.

These two selective pressures - food and predation - might act either in a complementary or antagonistic fashion. In either eventuality, they will have important consequences for breeding dispersion and success. In this chapter, habitat utilisation by Lapwings between their arrival on the breeding grounds and laying is investigated in relation to food availability and predation, and the adaptive significance of their habitat preferences discussed.

3.2 METHODS

Most observations on arrival, numbers and habitat utilisation during the pre-laying period were made in 1984 and 1985. Between the first recorded arrival and the beginning of laying, regular censusses were carried out on both sites: in 1984 nine were made on the arable site and 10 on the rough grazing site, while in 1985 nine were made on each. Census methods followed Galbraith and Furness (1981). Each census was carried out during early or mid-morning in fine, calm weather when display activity is most intense, and the same route was followed each time. The census routes ensured that all of each study area was visited, and that as much as possible of each site was counted from a vehicle (to minimise disturbance). Virtually all of the arable site and about 75% of the rough grazing site was accessible by vehicle. The remaining 25% of the rough grazing site was censussed on foot (during which, care was taken to cause as little disturbance as possible).

During each census the following were recorded:

a) the number and habitat distribution of birds in flocks. The arable habitats (i.e crops) are listed in Table 2.1 and the rough grazing habitats used by Lapwings comprised improved and unimproved land (2.1.2).

b) the number and habitat distribution of territories. Territories were identified by the presence of a male in either song flight or nest-scraping display (Cramp and Simmons 1983), or a nest with eggs. The territory habitat was that over which the males flew during song flight or within which their nest-scraping display took place or nests and eggs were situated. Where a song flight overlapped more than one habitat, the territory habitat was recorded as that which had the greatest representation within the area circumscribed by the flight path. The number of territories in each habitat was taken to be the maximum count obtained during a single census.

c) flock sex ratios. Using a vehicle as a mobile hide, it was often possible to approach flocks closely enough to determine the sex of individuals. Male Lapwings in typical breeding plumage can be distinguished by their longer crests and the purple sheen on their wing coverts. During the pre-nuptial moult the males also acquire a more clear-cut and contrasting black and white face pattern. The sexes can also be distinguished in flight since the males have a shorter outermost primary which gives their wings a characteristically rounded outline (Ennion 1949, Spencer 1953, Prater, Marchant and Vuorinen 1977).

In early February sex determination had to be based on crest length and covert colour alone, since there was little sexual display and many males had not completed their pre-nuptial moult. Because of this difficulty, my estimate of the proportion of females among flock birds in early February may be too high (since males with shorter crests or duller plumage could have been misidentified as females). It is not known whether females undergo a pre-nuptial moult since their winter and breeding season plumages are similar.

d) flock activity. The activity of birds in flocks was categorised as either feeding or resting (the latter included roosting and preening).

Lapwings usually rest with their bills tucked under their scapulars or with their heads hunched down on their shoulders. Although when feeding they are frequently motionless for periods of several seconds (before either moving on to a new feeding area or pecking at prey), their posture is quite different from resting birds since their heads are held high and often inclined at an angle to the ground surface (Metcalfe 1985). Whenever I was not certain whether a bird was resting or had merely paused between feeding movements, I watched it for approximately 20 seconds before directing my attention to the next bird. If in that time the individual did not show any sign of feeding it was categorised as resting.

e) feeding behaviour and diet. Observations on the feeding behaviour of individuals included: the duration of each observation bout (timed on a stopwatch), the total number of pecks made during the period, and the number of pecks that resulted in prey capture. Only observation bouts of three minutes or longer were included in the analyses.

Where possible, prey items were identified. The only items which were large enough to be identified at normal observation distances were medium and large-sized earthworms (Annelida: Lumbricidae); all others were classified as small items, although this category is likely to include smaller earthworms, as well as insects and their larvae.

The following definitions have been made: peck rate - number of pecks at ground per minute of observed foraging behaviour; intake rate - number of pecks per minute where an item of food was swallowed; success rate - percentage of pecks that resulted in food being swallowed.

3.3 RESULTS

3.3.1 Arrival, numbers and territory occupation

In 1984 and 1985 no birds were recorded at either study site during visits between August of the previous year and the end of January. First arrival on both sites took place during early February (Fig. 3.1) and numbers increased rapidly thereafter. Severe weather caused temporary reductions during a period of snow lie (rough grazing 1984), and when the ground surface was frozen for several consecutive days (arable 1985). Numbers at both sites peaked in March. On the arable site more birds were present during the March peaks than eventually stayed to breed, suggesting that it may be used as a stopover point by birds travelling to more distant breeding areas, or that some birds may be displaced to breed elsewhere.

At first, birds remained in flocks, but territory occupation began soon after first arrival and by the end of March the number of territories was more or less stable (Fig. 3.1). In the flocks on the arable site males outnumbered females among the first arrivals. The proportion of males then fell, presumably as the rest of the females arrived, and reduced still further as the males left the flocks and took up territories (Fig. 3.2). Due to the topography, the close approach necessary for sexing was not often possible on the rough grazing site. However, the few data that are available (Fig. 3.2) indicate that the flock sex ratio followed a similar pattern. Since the males are still moulting into their breeding plumage during February, sexing then is less easy than later in the season and the proportion of males shown in Fig. 3.2 is likely to be an underestimate.

3.3.2 Habitat use during the pre-breeding period.

Prior to the start of the breeding season, the day-time habitat use and activity of flock birds on the arable site showed a marked lunar periodicity. As the cycle approached the new moon, the proportion of birds found during the day on spring cereals declined while the proportion on pasture and hayfields increased (Fig. 3.3). The activities of birds in different crops differed significantly (Table 3.1): a higher proportion of birds in cereals spent their time "resting" (sleeping or preening), and a smaller proportion feeding than on hay or pasture.

Table 3.1. Day-time activities of Lapwings on different crop types on the arable site. () = % activity in each habitat. X^2 value calculated from raw data, e.g expected number feeding on spring cereals = 1469 x 1281 / 1928 = 976.

	SPRING CEREALS	HAY/ PASTURE	TOTAL BIRDS	
N^{O} FEEDING(%)	909(62.0)	372(81.0)	1281	X^2=57.5,2df,p<0.001
N^{O} RESTING(%)	560(38.0)	87(19.0)	647	
TOTAL BIRDS	1469	459	1928	

The choice of day-time feeding habitat on the arable site reflects the invertebrate biomasses in the different crop types (Table 3.2). Pasture and hay fields supported a significantly higher number and biomass of invertebrates than cereal fields (Mann-Whitney test: $z_{numbers}$= -4.55, p<0.0001; z_{biom}= -4.05, p<0.0001). These differences affected the the feeding rates of birds in cereal fields (Tables 3.3 and 3.4). Although Lapwings feeding in spring cereal fields had a significantly higher peck rate (Mann-Whitney test: U = 114.5, p<0.05), their intake rates were lower (though not significantly so) than birds on Hay/pasture (Mann-Whitney test: $U_{successful\ pecks}$ = 157, ns). Thus, to achieve similar intake rates, Lapwings feeding on spring cereal

fields had to expend more effort than birds feeding on hay/pasture.

Table 3.2. Mean numbers and dry weights(mg) of invertebrates in 1/25 m^2 soil samples in different arable habitats. () =s.d.

CROP	n	EARTHWORMS n/SAMPLE	d.w.	LEATHERJACKETS n/SAMPLE	d.w	OTHERS n/SAMPLE	d.w
S.CEREAL	15	5.1(4.713)	128	0.8(1.082)	5	0.4(0.737)	12
W.CEREAL	10	8.3(6.037)	467	0.8(1.475)	13	0.6(1.349)	1
HAY	20	10.3(8.176)	499	9.5(12.34)	91	1.4(1.602)	12
PASTURE	15	20.3(16.37)	881	15.5(14.08)	182	1.3(2.463)	7

Table 3.3. Feeding rates on the arable site during the pre-breeding period. Peck rate = pecks/minute; intake rate = items ingested/minute.

CROP	nOF BIRDS	n MINUTES OBSERVED	MEAN PECK RATE	MEAN INTAKE RATE	SUCCESS RATE OF PECKS
SPRING CEREAL	18	72.1	4.6	1.9	41%
HAY/PASTURE	19	85.7	3.7	2.3	62%

Table 3.4. Prey capture rates on the arable site during the pre-breeding period. "others" comprises items which were too small for identification and is likely to include smaller earthworms as well as insects and leatherjackets.

CROP	n OF BIRDS	n MINUTES OBSERVED	MEAN n WORMS/ MINUTE	MEAN OTHERS/ MINUTE
SPRING CEREAL	18	72.1	0.4	1.5
HAY/PASTURE	19	85.7	0.5	1.8

Lapwings on the rough grazing site also showed marked habitat preferences during the pre-breeding period. The adults fed almost exclusively on improved areas, where the prey biomass was greater (Table 3.5; Mann-Whitney test: $U_{numbers} = 96.0$, $p<0.01$; $U_{biom} = 68.5$, $p<0.001$).

Table 3.5. Mean numbers and dry weights(mg) of invertebrates in 1/25 m^2 soil samples from improved and unimproved rough grazing.()=s.d.

HABITAT	n	EARTHWORMS n/SAMPLE	d.w.	LEATHERJACKETS n/SAMPLE	d.w.	OTHERS n/SAMPLE	d.w
IMPROVED	18	2.3(2.824)	102	4.0(3.725)	32	7.7(29.30)	6
UNIMPROVED	20	0.9(2.605)	18	1.3(3.246)	11	1.3(1.814)	4

Lapwings feeding on improved land on the rough grazing site had a significantly higher peck rate, but they were no more successful and took smaller prey, than birds feeding on hay/pasture on the arable site (Tables 3.6 and 3.7; Mann-Whitney tests: $U_{peck\ rates} = 31.5$, $p<0.01$; $U_{worms/min} = 41.5$, $p<0.05$; $U_{others/min} = 55.0$, ns).

Table 3.6. Feeding rates on improved rough grazing and hay/pasture during the pre-breeding period. Peck rate = number of pecks/minute, intake rate = number of items ingested/minute.

CROP	n OF BIRDS	n MINUTES OBSERVED	MEAN PECK RATE	MEAN INTAKE RATE	SUCCESS RATE OF PECKS
IMPROVED R.G.	9	65.4	5.9	2.3	39%
HAY/PASTURE	19	85.7	3.7	2.3	62%

TABLE 3.7. Prey capture rates on improved rough grazing and hay/pasture during the pre-breeding period. "others" comprises items which were too small for identification and is likely to include smaller earthworms as well as insects and leatherjackets.

CROP	n OF BIRDS	n MINUTES OBSERVED	MEAN n WORMS/ MINUTE	MEAN OTHERS/ MINUTE
IMPROVED R.G.	9	65.4	0.2	2.1
HAY/PASTURE	19	85.7	0.5	1.8

3.3.3 Habitat use for nesting territories

The distribution of nesting territories on the arable site deviated significantly from random (with respect to crop distribution) in the two years when detailed censusses were carried out (Table 3.8; $X^2(1984) = 86.7$, $p<0.001$; $X^2(1985) = 78.2$, $p<0.001$, 5df in both cases). Lapwings on the arable site showed a highly significant preference for nesting in cereal fields over other crop types ($X^2(1984) = 81.70$, $p<0.001$; $X^2(1985) = 70.90$, $p<0.001$, 1df in both cases). Moreover, when the data from both years are combined, there is an indication of a preference for spring over winter cereals, although this is not statistically significant ($X^2 = 2.280$, 1df, $p<0.15$). No preference was shown between spring oats or barley ($X^2 = 0.743$, 1df, $p>0.60$).

Table 3.8. Distribution of nesting territories with respect to crop type on arable site. () = expected number of territories if their distribution was random with respect to crop distribution. Area in ha.

	1984		1985	
CROP	AREA	TERRITORIES	AREA	TERRITORIES
SPRING OATS	215	81 (40.7)	225	73 (34.7)
SPRING BARLEY	92	29 (17.4)	69	17 (10.6)
WINTER CEREAL	58	16 (11.0)	41	8 (6.4)
HAY/SILAGE	293	28 (55.4)	312	29 (48.1)
PASTURE	174	8 (32.9)	171	3 (26.6)
OTHER	24	0 (4.5)	38	2 (5.9)
TOTAL	856	162	856	132

Although Lapwings on the arable site nested mainly in cereal fields, their measured densities varied widely from field to field (Fig. 3.4). To examine causes of this variability a step-wise multiple regression analysis was carried out in which the nesting density in

each cereal field was the dependent variable and the independent variables comprised: $\log_{10}$ field area in ha (LAREA), $\log_{10}$ distance to closest short pasture (LDSP), LOG_{10} distance to closest public road (LDR), $\log_{10}$ distance to closest occupied building (LDB), $\log_{10}$ distance to closest trees or tall hedges (LDT) and the $\log_{10}$ number of years that the particular field had been under cereals (LAGE). These variables were chosen so that the influence of human disturbance (LDB, LDR), risk of predation (LAREA, LDT), tradition (LAGE) and proximity of suitable feeding habitat for adults and chicks (LDSP - pasture is an important feeding area for adults (see above) and short pasture is the preferred chick feeding habitat (see Chapter 6)) on nesting density could be investigated.

Only three of the independent variables contributed significantly to the total variance: LDT(23.0%), LDSP(20.8%) and LAREA(6.3%), giving an explained variance 50.1% of the total and a combined regression equation of: DENSITY = -66.12(LDSP) + 58.10(LDT) + 29.75(LAREA) + 17.56. When not transformed logarithmically, the three parameters explained only 35.8% of the total variance.

Lapwings nesting on the rough grazing site also showed significant habitat preferences, with virtually all nests situated on unimproved land (Table 3.9. $X^2(1984) = 9.320$, $X^2(1985) = 9.555$; $p<0.01$, 1df in both cases), the habitat in which food availability and feeding rates were lower.

Table 3.9. Distribution of Lapwing nesting territories with respect to habitat distribution on the rough grazing site. () = expected number of territories if their distribution were random with respect to habitat.

	1984		1985	
HABITAT	AREA(ha)	n TERRITORIES	AREA(ha)	n TERRITORIES
IMPROVED	16.2	2 (11.3)	16.2	2 (11.5)
UNIMPROVED	84.0	61 (51.7)	84.0	62 (52.5)

3.4 DISCUSSION

3.4.1 The pre-breeding period

In the period between arrival on the breeding grounds and egg laying the energy requirements of both male and female Lapwings are likely to be high. At this time the males are occupying territories and indulging in frequent and energetically expensive flight displays with, possibly, a reduced amount of time available for feeding. The females, on the other hand, require energy reserves for egg formation and incubation. These demands are met by feeding after dark and in the habitats where food is most plentiful:

a) nocturnal feeding: Lapwings are both diurnal and nocturnal feeders (Cramp and Simmons 1983) and, although their nocturnal behaviour has not been adequately investigated, there is evidence that night-time feeding is influenced by the lunar cycle. Spencer (1953) found that birds were active after dark mainly on nights close to the full moon. Milsom (1984) showed that nearer to the full moon a higher proportion of birds spent the day-time resting than when the moon was new. This was presumably because they were able to obtain a greater part of their daily food requirement nocturnally on the brighter nights of the full moon.

Outside the breeding season, Lapwings on farmland feed mainly on earthworms (Barnard and Stephens 1981, Thompson 1983), although

leatherjackets are also likely to be an important component of their diet (pers obs.). Both of these invertebrate taxa are most active and closest to the ground surface after dark (Darwin 1881, Laverack 1963, Tinbergen and Drent 1980) at which time their potential availability to Lapwings will be greatest. However, since Lapwings are visually hunting predators, the actual availability of their prey could depend largely on light conditions and, hence, the phase of the moon.

Prior to the breeding season, both diurnal habitat utilisation and activity on the arable site were influenced by the lunar cycle, presumably through its effect on the suitability of night-time feeding conditions. When the moon was large and the nights brighter and birds may have fed more successfully after dark, many spent the day-time roosting in cereal fields (where they were highly cryptic - much more so than on hay or pasture fields). During the new moon period when the nights are darker, night-time feeding is, presumably, less successful or may stop altogether, necessitating more intensive feeding during the day. At this time, more birds spent the day-time on hay or pasture fields, where food was more abundant, and a higher proportion of birds actively fed.

b) diurnal feeding habitat: during the pre-breeding period, the preferred diurnal feeding habitats on both study sites were those in which the prey biomasses and feeding success were highest. However, in spite of an increased effort (in terms of peck rates) the feeding success of birds on the rough grazing site was lower than on the arable site. This is a reflection of the lower prey biomass on improved rough grazing (the preferred feeding habitat) and has interesting implications for maternal body condition and egg size (Chapter 4).

3.4.2 Nesting habitat

The choice of nesting habitat on arable farmland and rough grazing is influenced by at least two factors: the crypticity of adults and nests (and, hence, the risk of predation), and the proximity of suitable feeding habitat.

a) predation: nest predation has been proposed as an important influence on Lapwing nesting distribution in two previous studies: in Holland Lapwings preferred to nest in pasture fields which were brown or grey in appearance because of the predominance of coarse grasses, and avoided the more fertile green fields (Klomp 1954). Klomp suggested that the ultimate value of this behaviour lies primarily in the lower height of the rough grasses later in the season, when the chicks hatch and move off in search of food. In the more fertile fields the grass would be too tall to allow easy chick movement. Klomp further proposed that nest crypticity might also be an important element in this choice of habitats. On farmland in Aberdeenshire, Elliot (1982) found that predation was an important influence on Lapwing nesting distribution and social organisation. As in the present study, birds did not nest close to trees, especially those which contained crow nests.

Predators of adult Lapwings on the arable and rough grazing study areas were known to include Sparrowhawks (Accipiter nisus) and Peregrine Falcons (Falco peregrinus) while potential predators seen regularly included Buzzards (Buteo buteo), Stoats (Mustella erminea), domestic cats (Felis sylvestris) and dogs (Canis familiaris). The commonest potential diurnal predator on eggs and chicks was the Carrion Crow (Corvus corone). Many of these, especially Carrion Crows, may use hedges and trees as vantage points or cover from which to locate Lapwing nests or broods.

On the arable site spring cereals comprised only 34% of the area under crops yet held 68% of nesting territories - a preference which could confer protection against predators. Prior to crop emergence, I found that, due to their cryptic colouration, incubating adults and their clutches were very difficult to locate against the bare, brown surface of the spring cereal fields. In contrast, birds incubating in hay stubble, winter cereal or pasture fields were comparatively conspicuous. An additional advantage of nesting on the relatively featureless surface of spring cereal fields is that when a sitting bird leaves the nest (this usually occurs at observer distances in excess of 150m), it is difficult to pin-point the nest position without fixed reference points. I found that nest-finding in pasture and hay fields was easier since there were usually tussocks, cowpats or some other landmark close to the nest. Presumably, the differing degrees of difficulty that I experienced in nest-finding in the different crops would be encountered by other visually hunting "predators" such as crows. The preference for large fields and the avoidance of those close to trees or tall hedges which could conceal predators is also likely to be a predator avoidance strategy.

Any anti-predation advantage gained from nesting in cereal fields on the arable site was, however, swamped by widespread clutch destruction during cultivation (Chapter 5).

On the rough grazing site birds nested almost entirely on unimproved land. This had a broken, patchy appearance due to hummocks, grass tussocks or clumps of rushes, and a generally brown or grey colouration due to the dominance of coarse grasses, sedges and moss. Improved rough grazing resembled pasture on the arable site in that the grasses were green in colour and were kept short by the intensive grazing of sheep and cattle. I found locating incubating adults difficult on unimproved land due to the cryptic background and the

longer vegetation, but much easier on improved land.

b) food availability: the food supply in the immediate vicinity of the nest was not an important influence on nesting habitat selection. Prey availability on the preferred nesting habitats on both study areas was comparatively low and chicks (Chapter.6) and off-duty adults left the nest site to feed on pasture (the arable site) or wet areas and improved rough grazing where invertebrates were more plentiful (Chapter 2). The distance between the nest site and suitable feeding habitat was, however, an important influence on nest site selection on the arable site. Birds preferred to nest in cereal fields close to pasture thus reducing the journey time of adults and chicks to feeding areas.

In summary, early in the nesting season crypticity of nests and incubating adults is of paramount importance and adults choose nesting habitats accordingly - Klomp's "brown" areas. Since the adults can feed off-territory, food availability in the immediate vicinity of the nest is not so important. Once the chicks hatch, however, they must move to areas where there is an adequate food supply. These are often the areas in which the off-duty adults fed during the incubation period and are more productive and greener in appearance. Safety from predators and food availability are, therefore, major constraints on the selection of habitats by Lapwings and result in the sequential utilisation of two rather different habitats during the course of the breeding season.

Figure 3.1.

Arrival, numbers and territory occupation at both study sites. Open symbols = 1984, closed =1985. Continuous lines = numbers, broken lines = territories. Territories were identified by the presence of either a nest or displaying male.

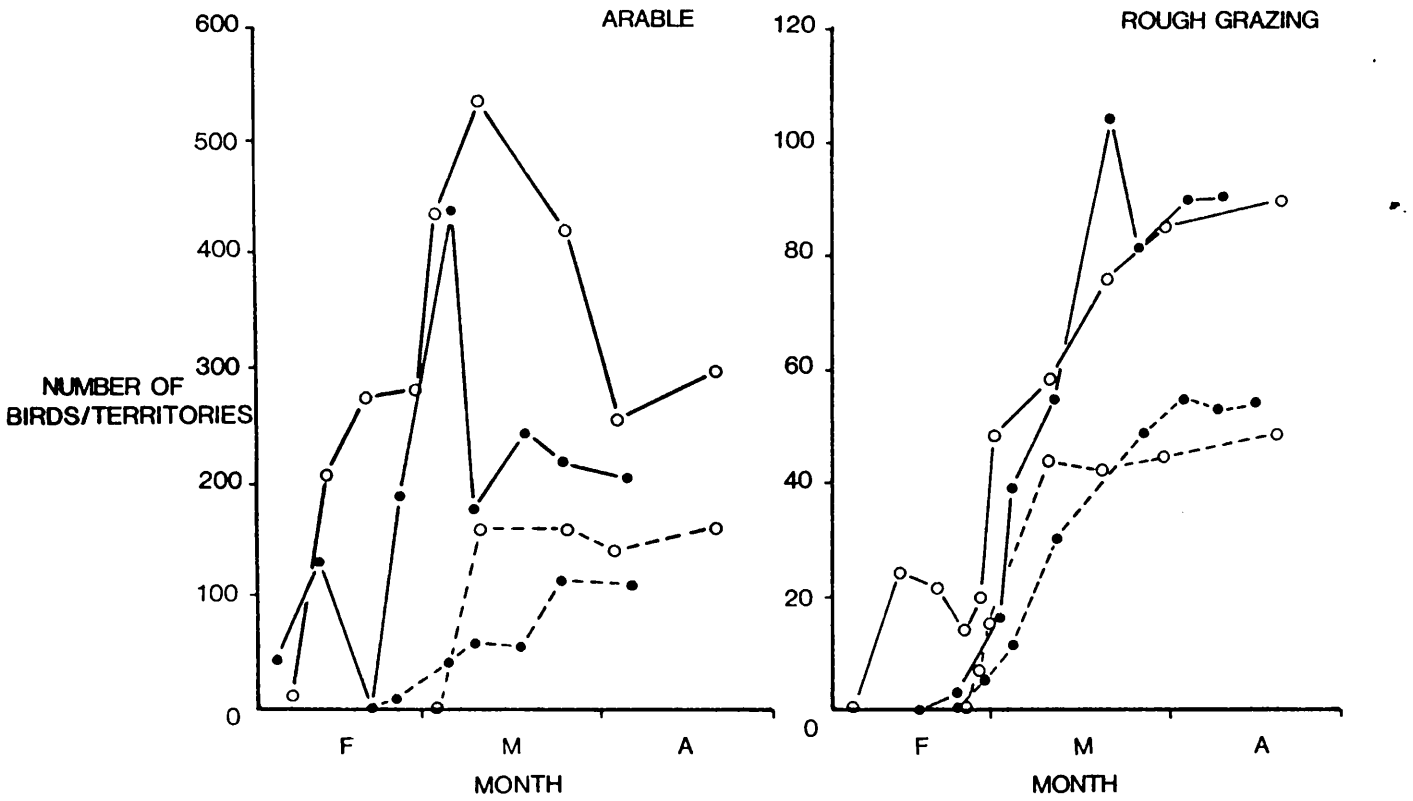

ARABLE
ROUGH GRAZING
NUMBER OF BIRDS/TERRITORIES
600
500
400
300
200
100
0
120
100
80
60
40
20
0
F
M
A
MONTH
F
M
A
MONTH

Figure 3.2

Sex composition in Lapwing flocks in the pre-breeding and early breeding season. Closed symbols = arable site, open symbols = rough grazing site.

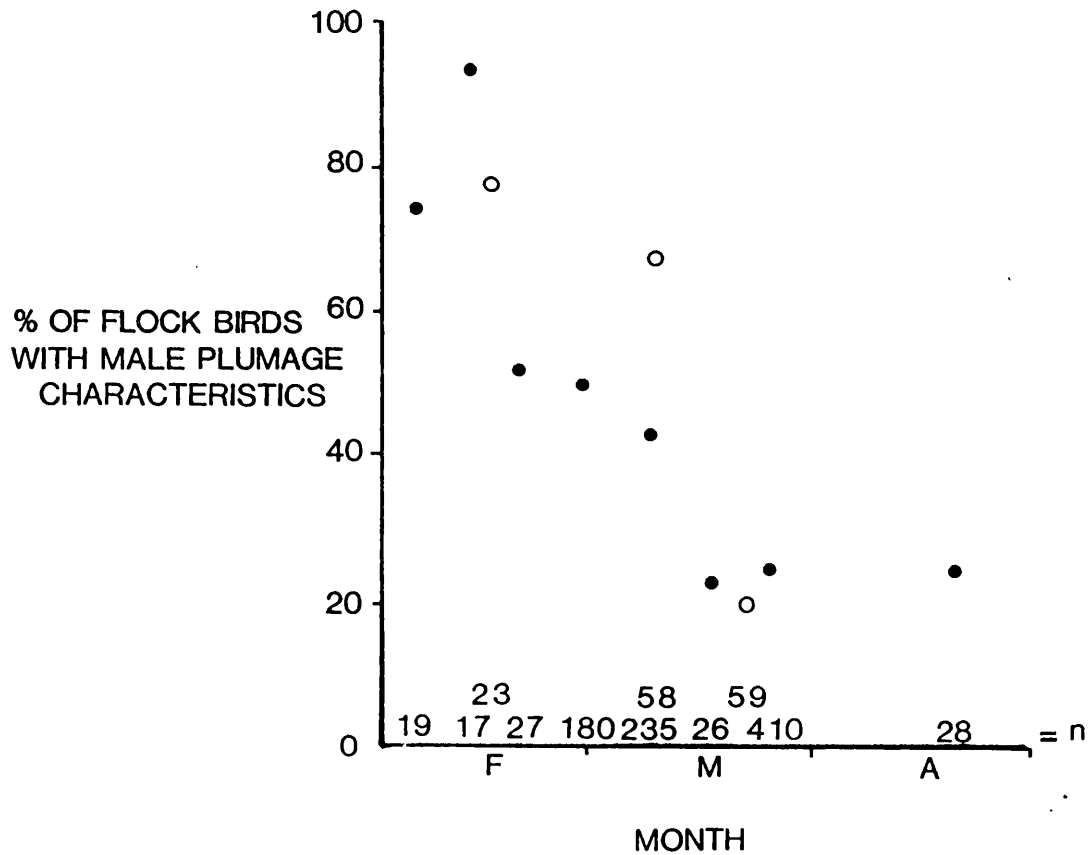
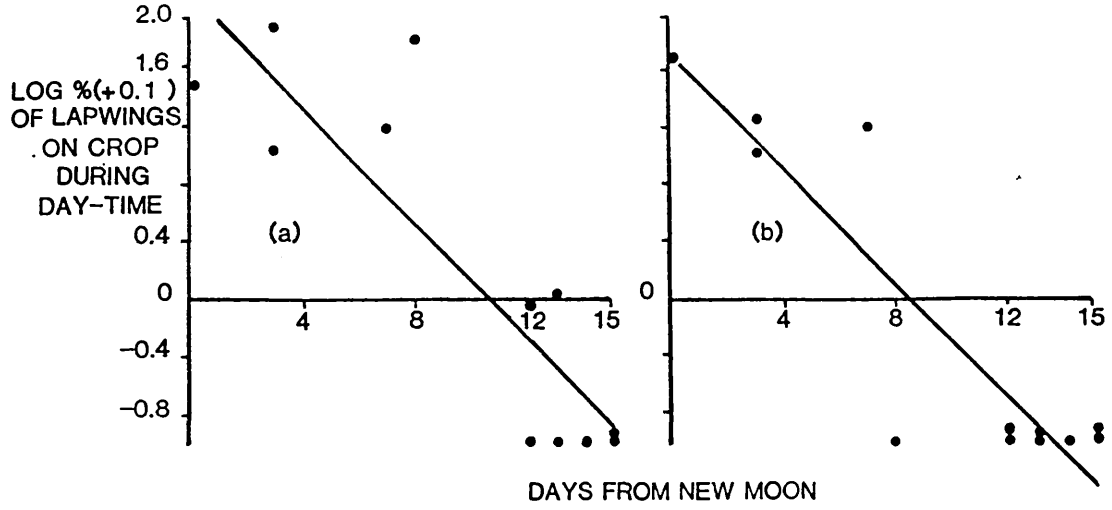

100
80
60
40
20
0
% OF FLOCK BIRDS WITH MALE PLUMAGE CHARACTERISTICS
19 17 23 27 180 235 58 26 59 410 28
= n
F
M
A
MONTH

Figure 3.3

Day-time use of crops in relation to lunar cycle by Lapwings on the arable site. (a) = hay/silage, (b) = pasture, (c) = spring cereals. Whereas logarithmic relationships were found to fit the data best for hay/silage and pasture, a linear relationship fitted best for spring cereals. All regressions were carried out on the arc-sine transformations of the percentage values and fitted using the method of least squares: a) $y = -3.71x + 55.27$; $r = -0.70$, $p<0.02$. b) $y = -2.52x + 35.4$; $r = -0.89$, $p<0.001$. c) $y = 5.54x + 10.76$; $r = 0.93$, $p<0.001$. $n = 12$ in all three cases.


2.0
1.6
LOG %(+0.1)
OF LAPWINGS
ON CROP
DURING
DAY-TIME
0.4
0
−0.4
−0.8
(a)
(b)
4
8
12
15
DAYS FROM NEW MOON

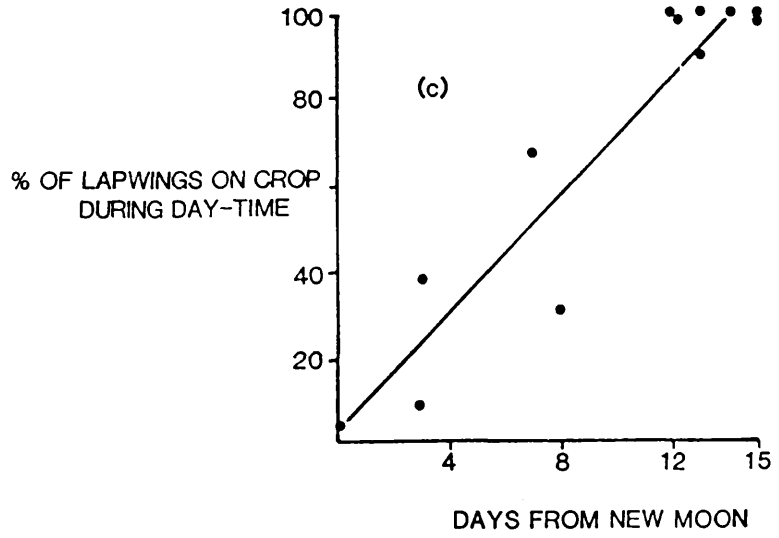
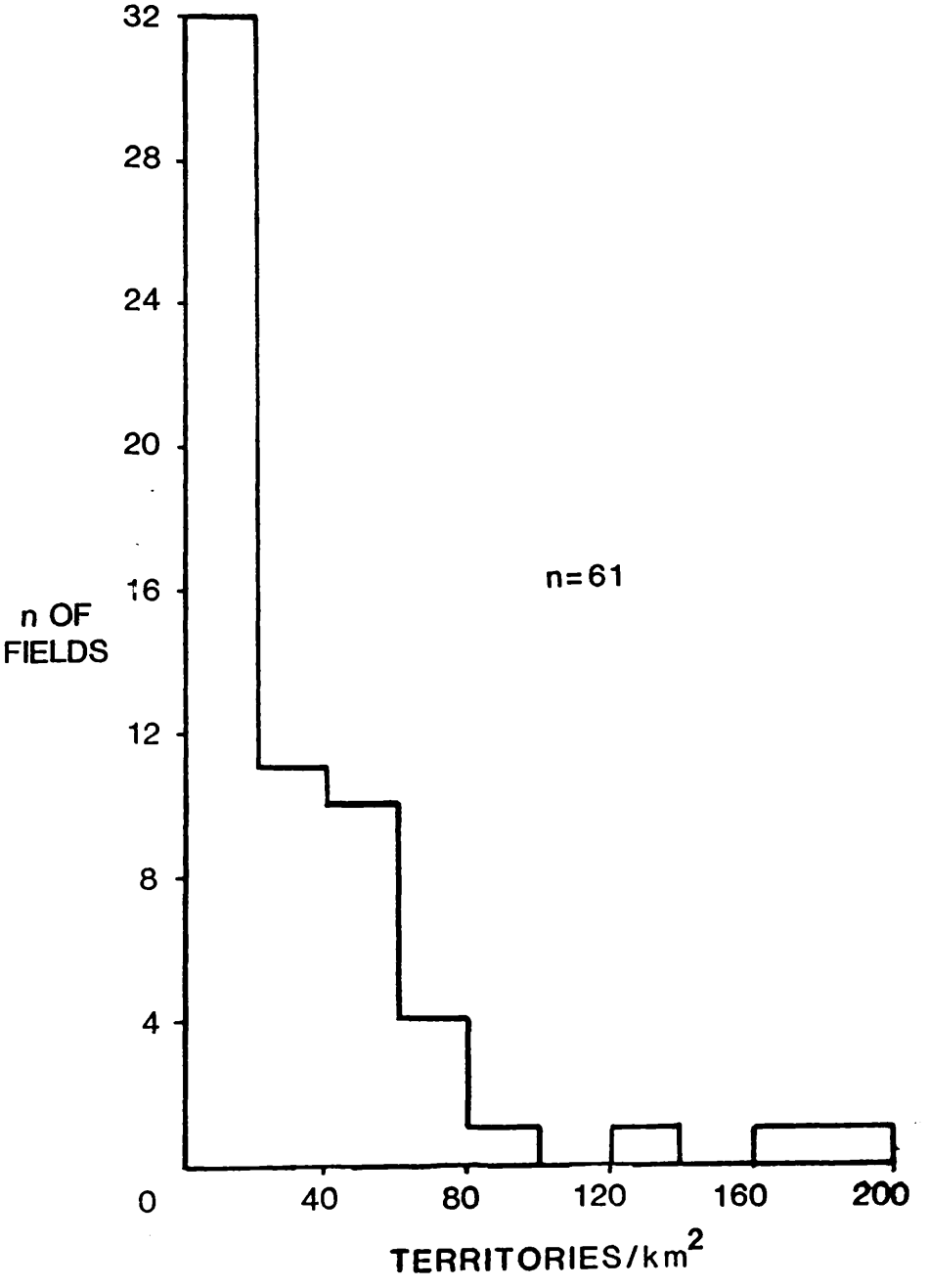

100
80
40
20
% OF LAPWINGS ON CROP
DURING DAY-TIME
(c)
4
8
12
15
DAYS FROM NEW MOON

Figure 3.4

Territory densities in cereal fields (1984 and 1985 combined). Territories were identified by the presence of either a nest or a displaying male. n = 61 fields.


32
28
24
20
16
12
8
4
0
n OF FIELDS
n=61
40
80
120
160
200
TERRITORIES/km2

Chapter 4. EGGS AND LAYING

4.1 INTRODUCTION

During the different stages of the breeding cycle birds may improve their chances of reproductive success by: breeding at the best time of the year relative to the food requirements of the laying female and the young; producing the optimal clutch size, i.e that which will result in the greatest number of independent young during the parent's lifetime, and adequately provisioning and protecting the young during their nestling and fledgling stages (Perrins and Birkhead 1983).

The relative importance of the parental contribution to the success of each stage of the reproductive process, and, hence, the parents' ability to influence overall breeding success, varies depending on the mode of development of the chicks. Chick survival depends on extrinsic factors such as weather and intensity of predation, and on aspects of their own intrinsic "quality" e.g size, or protein and lipid reserves. Parents of altricial young can directly influence the quality of their young after hatching by maximising the rate at which food is brought to them and by providing them with a diet suited to their needs. The parents of self-feeding precocial chicks are, however, constrained in their ability to directly influence chick quality after hatching, although a high level of parental attention is still necessary to guard against extrinsic factors (Walters 1982). Consequently, parental behaviour and indirect investment in chick quality prior to hatching assume a greater degree of importance. In addition to breeding at the best time of year and producing the optimum clutch size, precocial birds may improve the quality of their chicks, and thereby their own prospects of breeding successfully, by adequately provisioning them for life after hatching while they are still in the egg. Since the ability of parent birds to

invest in egg quality presumably depends on the available food supply during the pre-laying period, as well as on stored reserves, habitat quality might exercise an indirect, as well as a direct effect, on chick quality and survival.

Various studies have shown that there is a general relationship between the relative size and biochemical composition of avian eggs and the stage of development of the chicks at hatching. Species which produce down-covered hatchlings (i.e chicks which are either precocial or left unattended in the nest for long periods such as seabirds and raptors) lay eggs which are large relative to the weight of the female (Rahn et al. 1975, O'Connor 1984). As well as being relatively large, the eggs of precocial birds have higher energy densities since they have proportionately more yolk and lipid and less albumen and water than eggs of altricial species (Romanoff and Romanoff 1949, Ricklefs 1977, Carey et al. 1980). This relationship between egg size and composition, energy content and hatchling precocity is generally thought to be adaptive: since they are mobile and usually self-feeding, precocial chicks must hatch at a comparatively advanced developmental stage and retain large enough yolk reserves to sustain them during the first few days after hatching. Both requirements depend on a high maternal energy investment in each egg.

Intra-specific egg size variation has also been shown to be an important influence on chick viability. Chicks from larger eggs may be structurally larger and/or have larger yolk reserves (Parsons 1970, Ricklefs et al. 1978, Ricklefs 1984, Ankney 1980, Birkhead and Nettleship 1984), grow more quickly (Schifferli 1973, Davis 1975, O'Connor 1975, Murphy 1985), or survive better (Davis 1975, Parsons 1975, Howe 1976, Nisbet 1978, Lundberg and Vaisanen 1979, O'Connor 1979, Ankney 1980).

Since Lapwings, like most other waders, have precocial chicks which feed themselves (Hale 1980), the timing of breeding, clutch size, and egg size and quality might be expected to influence breeding success and, ultimately, population processes. In this chapter the factors affecting these parameters in both the rough grazing and arable habitats are investigated.

4.2 METHODS

4.2.1 Estimation of first egg dates

First egg dates (the date on which the first egg of a clutch was layed) and expected hatching dates were obtained by one of two methods:

a) if the clutch was found prior to the last egg being layed, the first egg and clutch completion dates were calculated on the assumption that the laying interval between successive eggs was two days. Due to the difficulty of finding nests with incomplete clutches, and because of the disturbance caused by repeated visits to nests during laying, the actual laying interval was not investigated. However, as published estimates vary between one (Klomp 1951) and 2.8 days (Heim 1974), any errors incurred by assuming an interval of two days are likely to be small. The expected hatching date of each clutch was estimated as 25 days after clutch completion, since that is the average incubation period (see 4.3.6).

b) most nests were found after the last egg had been layed, and the first egg and expected hatching dates of these were estimated from the mean egg density (mean egg weight/mean egg volume). The density of avian eggs decreases during incubation due mainly to water loss (Drent 1970, Rahn and Ar 1974). Once the relationship between density and stage of incubation has been determined in eggs of known hatching date, the laying date and time till hatching of eggs in nests found

after clutch completion can be estimated (Furness and Furness 1981).

The value of egg density measurements in estimating the stage of incubation of Lapwing clutches and wader clutches in general has been discussed by Green (1984) and Galbraith and Green (1985).

The relationship between mean egg density and stage of incubation in 60 Lapwing clutches of known hatching date in 1984 and 1985 is shown in Fig. 4.1. During incubation, these eggs lost, on average, 16.8% of their fresh weight (Fig. 4.1), which is close to the 17% proposed by Rahn and Ar (1974) for birds in general. In 1984 the clutches on the arable site lost weight significantly more quickly than those on the rough grazing site (ANCOVA: $F_{slopes} = 4.966$, 2 and 29 df, $p<0.05$), however, the rates of weight loss were not significantly different in 1985 (ANCOVA: $F_{slopes} = 0.117$, 2 and 19 df), or when both years are combined (ANCOVA: $F_{slopes} = 1.469$, 2 and 54 df).

Although the hatching dates of clutches found after clutch completion can be obtained from Fig. 4.1, it is statistically more correct to regress days till hatching (y axis) against mean egg density. This operation gives a predictor equation of: days till hatching = 150.84density - 140.68 ($r = 0.905$, $p<0.001$) with a likely mean error (the mean deviation from the regression line) of 2.3 days (s.d = 1.876).

Once the hatch date of each clutch of unknown age had been estimated, the first egg date was calculated by assuming an incubation period of 25 days and a laying interval of two days between each egg. Egg density was only used to estimate clutch hatching date if neither laying dates nor hatching dates were obtained by observation.

4.2.2 Egg composition

During April 1985 40 freshly laid eggs were collected (under licence) from first clutches on both study sites. They were weighed (= fresh weight), measured, hard boiled, individually sealed in latex bags to reduce water loss during storage, and frozen to await analysis. Each egg was subsequently separated into shell, yolk and albumen components. Each of these was weighed (to the closest 10mg), dried to constant weight in an oven at 70°C then reweighed to determine water loss. The lipid fractions of the yolks and 10 albumen samples were determined by extraction in a Soxhlet apparatus using boiling chloroform as a solvent.

Since some water loss occurred during storage and some of the albumen often adhered to the shell during separation, the albumen fresh weight was taken as: fresh egg weight - (shell dried weight + yolk fresh weight).

The allometric relationships among the various egg components were investigated by regressing the logarithms of their weights against the logarithm of the egg fresh weight. Using this method, a slope of 1.0 indicates that the component increases in direct proportion to egg mass. Slopes greater or less than 1.0 indicate that the proportion of the component becomes respectively greater or less with increasing egg mass.

4.3 RESULTS

4.3.1 Factors affecting the timing and duration of the laying period

a) habitat: despite the 150m difference in altitude (with associated climatic changes) the commencement of laying on the two study sites differed little in timing (Figs. 4.2 and 4.3). There is, however, evidence that the laying season stopped earlier on the arable site.

Whereas laying extended well into May on the rough grazing site, on the arable site it was virtually over by late April (Fig. 4.3). The preferred nesting habitat on the arable site was spring cereals (Chapter 3). In early April when crop growth is in its early stages, spring cereals are a suitable nesting habitat. By May, however, the crops were up to 20cm high, by which time cereals were no longer suitable as a nesting habitat (Lapwings have evolved as open-country nesting birds and appear to require uninterrupted views from the nest). The clutches which were begun on the arable site in mid - late May (shown hatched in Fig. 4.2) are further evidence that crop growth may truncate the laying season. These were all layed in fields which had been cultivated abnormally late in the spring (about six weeks later than normal). Furthermore, two of these three clutches were layed by females which had earlier failed on more typical cereal fields. During the intervening period these birds had been seen in various parts of the study area, but were not, apparently, breeding.

b) weather: despite April and May 1986 being much wetter than in the two previous years, egg laying was not delayed (Figs. 2.2 and 4.4). In 1984 and 1985 the beginning of laying coincided with the start of a consistent rise in air temperature (Fig. 4.5). In 1986 this temperature rise was delayed by about 20 days yet laying began as normal (Fig. 4.5). There is, therefore, little evidence of any relationship between weather conditions and the beginning of laying.

4.3.2 clutch size

Information on completed clutch sizes was collected mainly in 1984 and 1985 and the clutch size distributions in the two study areas are shown in Table 4.1 and Fig. 4.6.

Table 4.1. Clutch size distribution during 1984 and 1985. Nests begun on spring cereal fields prior to 10th April are excluded from the arable sample since it is likely that their clutch sizes were affected by disturbance during cultivation (see below). () = % frequency.

	CLUTCH SIZE				
	1	2	3	4	5
ROUGH GRAZING	0	4(3.3)	23(19.0)	94(77.7)	0
ARABLE	0	4(4.7)	14(16.5)	66(77.6)	1(1.2)
BOTH SITES	0	8(3.9)	37(18.0)	160(77.7)	1(0.4)

It is possible that the frequencies in Table 4.1 and Fig. 4.6 differ from those at the time of clutch completion due to partial predation of nests. However, the frequencies in nests checked within five days of clutch completion (as estimated from known hatch date or egg density) and less likely, therefore, to have been predated (assuming that the likelihood of predation increases with the length of time that the nest is available to predators), and in clutches checked later in incubation are not significantly different (Table 4.2). The frequencies of clutch sizes in Table 4.1 are likely, therefore, to be similar to those at clutch completion.

Table 4.2. Clutch size frequencies in nests checked within five days of clutch completion compared with nests checked later in incubation. () = expected numbers if the clutch size frequencies in both groups conformed to a common frequency distribution (the null hypothesis of the Chi Square test. Nests begun on spring cereals before 10th April are excluded (see text and Table 4.4).

	CLUTCH SIZE		
	<3	3	4 OR MORE
ALL OTHER CLUTCHES	5(3.4)	16(15.8)	67(68.8)
5 DAY CLUTCHES	3(4.6)	21(21.2)	94(92.2)

$X^2 = 1.40$, 2df, $p>0.50$

There were no significant differences in clutch sizes between the two study sites (Table 4.3). However, when the frequencies in different arable crops were compared (Table 4.4) significantly fewer than expected clutches of four eggs, and significantly more than expected smaller clutches, were found in nests begun in cereal fields before 10th April. This difference does not persist in later clutches and is likely to be caused by egg losses due to cultivation coinciding with laying.

Table 4.3. Clutch size frequencies in the two study areas. () = expected numbers if the clutch size frequencies on both sites conformed to a common distribution (the null hypothesis of the Chi Square test). Nests begun on spring cereals before 10th April are excluded (see text and Table 4.4).

	CLUTCH SIZE		
	3	4	OTHER
ROUGH GRAZING	23(21.7)	94(94.0)	4(5.3)
ARABLE	14(15.3)	66(66.0)	5(3.7)
	X^2 = 0.571, 2 df, p>0.80		

Table 4.4. Clutch size frequencies in cereals and hay+pasture on the arable site during two time periods: clutches begun before, or clutches begun on or after 10th April. () = expected numbers if the clutch size frequencies in each crop type and time period conformed to the common frequency distribution for that time period (the null hypothesis of the Chi Square test).

	CLUTCH SIZE			
	BEFORE 10th APRIL		AFTER/ON 10th APRIL	
	4	OTHER	4	OTHER
CEREALS	10(14.0)	12(8.0)	29(29.4)	12(11.6)
HAY+PASTURE	32(28.0)	12(16.0)	32(31.6)	12(12.4)
	X^2 = 4.710, 1df, p<0.05		X^2 = 1.257, 1df, p>0.80	

During the three years of the study there were differences in the relative proportions of different clutch sizes. The most marked of

these was a higher proportion of clutches of less than three eggs on both study areas in 1986 (Table 4.5). These differences were not, however, statistically significant.

Table 4.5. Annual variation in clutch size frequencies on both study sites. () = % representation in each year and habitat. The expected frequencies for the Chi Square test were calculated on the assumption that the the data conformed to a common frequency distribution for all three years combined.

	CLUTCH SIZE			
	ROUGH GRAZING		ARABLE	
	4	OTHER	4	OTHER
1984	50(74.6)	17(25.4)	40(66.7)	20(33.3)
1985	45(81.8)	10(18.2)	36(76.6)	11(23.4)
1986	21(67.8)	10(32.2)	13(52.0)	12(48.0)
	X^2 = 2.279, 2df, p<0.40		X^2 = 4.424, 2df, p<0.15	

There were no significant differences between first and replacement clutches (i.e. relayings after the loss of the preceeding clutch) laid by individual females in the same year (Table 4.6). Moreover, dividing the clutch size data into two time periods: clutches begun before or after 30th April, failed to reveal any significant seasonal trends (X^2_{arable} = 0.38; $X^2_{r.g}$ = 0.27; p>0.40, 1df).

Table 4.6. Clutch sizes laid by individual females in first and replacement nests. () = expected numbers if the frequencies in first and replacement clutches conformed to a common distribution (the null hypothesis of the Chi Square test).

	CLUTCH SIZE	
	4	OTHER
FIRST CLUTCHES	16(17.0)	5(4.0)
REPLACEMENT CLUTCHES	18(17.0)	3(4.0)
	X^2 = 0.618, 1df, p>0.50	

4.3.3 Egg size

Most egg measurements were made in 1984 and 1985. The distributions of egg volumes and mean egg volumes within clutches are shown in Fig.4.7.

Components of egg size variation. The components of the total egg size variation attributable to differences between females, and variability within clutches were investigated by carrying out separate one-way analyses of variance on eggs from first and replacement clutches (Sokal and Rohlf 1969). Splitting the data in this way eliminated any complication due to repeat layings by individuals.

In both first and replacement clutches on the rough grazing site egg size varied comparatively little within clutches and most of the observed variation was due to differences between females (Table 4.7). The pattern on the arable site was similar, except that there was a greater amount of variation within clutches and this became even more marked in replacement clutches.

Table 4.7. The percentages of the total variation in egg volume attributable to between-female and within-clutch components. "rep" = replacement clutches, () = the number of clutches in each category. F(first clutches): a) r.g = 8.935, 66 and 172 df; b) arable = 7.352, 54 and 141 df; F(replacements): a) r.g = 8.329, 22 and 57 df; b) arable = 5.820, 14 and 43 df; p(all cases)<0.001).

	HABITAT AND CLUTCH NUMBER			
	ROUGH GRAZING		ARABLE	
	1st(67)	rep(23)	1st(55)	rep(15)
FEMALES	69.2	67.1	64.0	55.4
CLUTCHES	30.8	32.9	36.0	44.6

Factors influencing egg size: a) Clutch number. The mean egg volumes in first and replacement clutches are compared in Table 4.8. Whereas mean egg volumes did not vary significantly between first and replacement clutches on the arable study area, there was a significant

reduction in volume on the rough grazing site.

Table 4.8. Mean egg volumes in first and replacement ("rep") clutches on each study area. n = number of clutches in each category; () = s.d.

		n	MEAN EGG VOLUME (ml)	
a) ROUGH GRAZING:	1st CLUTCHES	67	23.5(1.533)	t=-2.12, 88df, p<0.05
	REP CLUTCHES	23	22.7(1.521)	
b) ARABLE:	1st CLUTCHES	55	24.0(1.514)	t=0.33, 68df, p>0.70
	REP CLUTCHES	15	23.9(1.888)	

b) Season. Mean egg volumes did not correlate significantly with first egg dates on the arable study area ($r = -0.09$, 103 df, $p>0.15$). However, on the rough grazing site there was a non-significant negative correlation corresponding to an average reduction in mean egg volume of 0.76ml between the beginning and end of the laying season ($r = -0.13$, 118 df, $p<0.10$). This is similar to the difference between first and replacement clutches already noted for the rough grazing study area (0.8ml - Table 4.8). Furthermore, since the mean egg volumes in known first and replacement clutches on the rough grazing study area show no significant correlation with first egg dates ($r_{first} = 0.02$, 65 df, $p>0.40$; $r_{second} = 0.16$, 21 df, $p>0.15$), it is likely that the apparent seasonal reduction in egg volume on the rough grazing site is due merely to a higher proportion of replacement clutches later in the season.

c) Habitat. Eggs laid in the arable study area were larger than those from the rough grazing study area in both first and replacement clutches (Table 4.8). The difference was greater in replacement clutches due to the size reduction in rough grazing eggs between nesting attempts (1st clutches: $t = -1.80$, 120 df, $p<0.10$;

replacements: $t = -2.45$, 36 df, $p<0.05$).

d) Clutch size. The mean egg volumes in the three most frequent clutch sizes are compared in Table 4.9. There was a tendency for mean egg volume to increase with clutch size in both habitats, however, this trend was significant only on the arable site (ANOVA: $F_{r.g} = 1.16$, 2 df, $p>0.30$; $F_{arable} = 3.27$, 2 df, $p<0.05$). The mean volumes of eggs in arable clutches of three and four were not significantly different ($t = -0.47$, 94 df), however, eggs in arable clutches of two were significantly smaller than those in larger clutches ($t = -2.71$, 102 df, $p<0.01$). Thus, Lapwings on the arable site which laid clutches of two eggs produced smaller eggs than those birds which laid larger clutches.

Table 4.9. Mean egg volumes in different clutch sizes. n = number of clutches in each category. () = s.d.

	CLUTCH SIZE	n	MEAN EGG VOLUME (ml)
a) ROUGH GRAZING:	2	9	22.9 (1.095)
	3	25	23.1 (1.489)
	4	82	23.5 (1.520)
b) ARABLE:	2	8	22.7 (1.911)
	3	31	23.8 (1.477)
	4	65	24.0 (1.148)

e) Years. No significant differences in mean egg volume were found between the two years in which most of the egg measurements were collected (Table 4.10).

Table 4.10. Mean egg volumes in clutches in 1984 and 1985 in each study area. n = number of clutches in each category; () = s.d.

		n	MEAN EGG VOLUME(ml)	
a) ROUGH GRAZING:	1984	74	23.4(1.655)	
				t=0.41, 118df, p>0.60
	1985	46	23.3(1.246)	
b)ARABLE:	1984	60	23.7(1.300)	
				t=0.58, 103df, p>0.50
	1985	45	24.0(1.443)	

f) Female size and body condition. Table 4.11 displays the correlation coefficients obtained when the body measurements of 18 female Lapwings trapped during incubation in 1984 and 1985 were plotted against the mean egg measurements of their clutches.

Table 4.11. Correlation coefficients between the body measurements of 18 incubating female Lapwings and the mean egg volumes of their clutches. + = p<0.05, ++ = p<0.01, +++ = p<0.001).

	ADULT FEMALE MEASUREMENTS					
	WING LENGTH	HEAD & BILL	BILL LENGTH	FOOT LENGTH	WEIGHT	WEIGHT/ WING
MEAN EGG LENGTH	0.09	0.29	-0.14	0.50+	0.69+++	0.66++
MEAN EGG BREADTH	-0.13	0.05	-0.25	0.04	0.41+	0.44+
MEAN EGG VOLUME	-0.08	0.15	-0.26	0.21	0.59++	0.56++

Assuming that the weights of the incubating females are closely related to their weight at egg-laying, there is little evidence that maternal body size (denoted by wing, head and bill, bill and foot measurements) affects egg size. Female weights and body condition (weight/wing length) show significant positive correlations with egg length, breadth and volume (Table 4.11 and Fig. 4.8). This suggests that the size of the laying females is not important in determining egg size but that their body condition is. This was investigated

further using partial correlation analysis: the mean egg volume plotted against maternal weight gave a correlation coefficient of 0.59 (Table 4.11). When this operation was repeated but with maternal size (denoted by head and bill, foot and wing length) held constant, the resulting partial correlation coefficients were little changed at 0.58, 0.57 and 0.60, respectively. Female size, therefore, has little influence on egg sizes which are determined partly (36% of the variation explained) by maternal body condition.

Squaring the correlation coefficients in Table 4.11 shows that maternal body condition explains about 43% of the variation in egg length but only 19% of the variation in egg breadth. It seems, therefore, that egg volume is at least partly dependent on maternal body condition and that good condition is expressed in egg volume mainly through an increase in egg length rather than breadth. Fig. 4.9 shows that there is a marked, disproportionate increase in egg length with increasing volume (t-test comparing the mean shape indices of eggs <20 and >26 ml in volume: $t = 2.18$, 67df, $p<0.05$). Thus, larger eggs tend to be longer than smaller eggs.

Eight females trapped during incubation between 1984 and 1986 on the rough grazing site were in generally poorer body condition than 13 incubating females on the arable site (0.977 and 1.029, respectively; Mann-Whitney $U = 27.5$, $p<0.10$). It has already been shown (Chapter 3) that adult feeding success during the pre-laying period is lower on the rough grazing site and that eggs on the rough grazing site are smaller (Table 4.8).

4.3.4 Egg composition

Percentage composition. The mean percentage composition of 40 eggs is shown in Table 4.12, and the distribution of water, lipids and solids (protein, carbohydrate and inorganic material) among the two main egg

components is shown in Table 4.13.

Table 4.12. The percentage composition of eggs from the two study sites. The values were obtained from the fresh weight of each component and the fresh weight of the complete egg prior to separation. () = s.d.

	n EGGS	MEAN %YOLK	MEAN %ALBUMEN	MEAN %SHELL
ROUGH GRAZING	8	33.9(2.00)	60.6(1.70)	5.5(0.40)
ARABLE	32	32.8(2.20)	61.5(2.30)	5.7(0.50)
BOTH	40	33.1(2.20)	61.3(2.20)	5.6(0.50)

Table 4.13. The percentage composition of the two main egg components (solids = proteins, carbohydrates and inorganic materials).

	n EGGS	%WATER	%LIPID	%SOLIDS
YOLK	40	50.9	32.4	16.7
ALBUMEN	40	87.9	0.5	12.6

Egg size and composition. The results of the log-log plots of the egg components against fresh egg weight are shown in Table 4.14. Whereas the slope of the albumen fraction was significantly greater than 1.0 ($p<0.02$), that of the yolk and shell were significantly less than 1.0 ($p<0.05$). This indicates that the proportion of albumen increases with egg size but the proportions of shell and yolk decrease (although all three components show an absolute weight increase with egg size). Whereas the amount of solids in the albumen increased in direct proportion to egg size, the albumen water content increased disproportionately. The solids in the yolk increased in proportion to egg size, while the yolk lipid proportion fell. These relationships are presented graphically in Fig. 4.10.

Table 4.14. Results of regressing log egg component weights against log fresh egg weight. r = correlation coefficient; $R^2 = r^2 \times 100$; b = slope; s_b = standard error of b; A = the intercept.

	STATISTICS					
	r	p	R^2	b	s_b	A
YOLK	0.48	<0.01	22.9	0.62	0.18	0.06
ALBUMEN	0.90	<0.001	81.4	1.24	0.09	-0.56
DRY SHELL	0.30	<0.05	9.3	0.45	0.23	-0.47
YOLK WATER	0.32	<0.05	10.5	0.57	0.27	-0.16
YOLK LIPID	0.35	<0.05	12.1	0.47	0.21	-0.22
YOLK SOLIDS	0.54	<0.001	29.3	1.17	0.29	-1.50
ALBUMEN WATER	0.89	<0.001	79.2	1.27	0.10	-0.65
ALBUMEN SOLIDS	0.59	<0.001	35.2	1.08	0.24	-1.25

4.3.5 Egg size, chick size and survival

Heavier chicks hatch from large eggs (Fig 4.11). Hatchlings from larger eggs could be heavier because: a) they have greater reserves of protein, lipid, carbonydrate or water; b) because they are structurally larger; c) because they have denser coverings of down than those from smaller eggs. Since the head and bill length (but not the foot length) of hatchlings was significantly correlated with the mean egg volume of the clutch from which they hatched ($r = 0.48$, $n = 37$), at least part of the variability in hatchling body mass is explained by structural size. Without sacrificing chicks it was not possible to investigate the relationships between egg size, chick body size and composition directly. However, hypotheses a) and b) were tested indirectly using a hierarchical multiple regression analysis where the relative contributions of hatchling size and mean egg volume (i.e the contribution that egg size makes to chick weight over and above that of size) to the total variation in chick body mass were assessed. The cube of hatchling head and bill length (functioning as

an index of body size - volume is proportional to the cube of linear measurements) was entered into the analysis as the first independent variable, followed by mean egg volume. Hatchling size explained 28.7% of the variation in body mass, while mean egg volume explained a further 26.9%. Heavier hatchlings, therefore, are heavier because they are larger and because they are heavy for their size, i.e they are either carrying greater reserves of protein, carbohydrate, lipid or water, or have denser coverings of down. Since, however, the down from an accidentally killed hatchling weighed only 0.26g (about 1% of body weight), it is extremely unlikely that variation in down density could explain more than a tiny proportion of the effect of egg size on chick body weight.

The allometric relationship between egg volume and hatchling weight was investigated by regressing the logarithm of chick weight against the logarithm of the mean egg volume in the clutch from which it hatched. The slope of the regression was not significantly different from 1.0 ($b = 1.09$, $s_b = 0.19$), which indicates that large eggs do not produce disproportionately heavy chicks.

Chick survival in relation to egg size was investigated using data from 1985 rough grazing nesting attempts. Arable data were not included because the survival pattern was influenced largely by anthropogenic factors (see Chapters 5 and 6), and because chick survival on the arable site was low and sample sizes correspondingly small. 1984 data have been excluded since that was the first year of the study and the chick survival estimates are unlikely to be as accurate as those obtained later. The clutches were separated into two categories on the basis of their mean egg volumes, and the fates of the resulting chicks from each compared using Chi Square tests. Initially the clutches were separated about a position (23.5ml) which ensured approximately equal sample sizes. This was then raised and

lowered by 0.5ml to guard against the risk of an arbitrary choice of categories resulting in artificially significant results (Table 4.15).

Survival to fledging was better among chicks from clutches with greater mean egg volumes (Fig. 4.12, Table 4.15). Table 4.15 shows that egg size enhanced chick survival to fledging through its effect in the first 10 days after hatching. Beyond that age egg size had no significant effect.

Table 4.15. Numbers of chicks which died or survived from 1985 rough grazing clutches categorised in three alternative ways according to the mean egg volumes of the clutches from which they hatched. a) between hatching and 10 days old; b) between hatching and 35 days old (i.e fledging); c) between 10 and 35 days after hatching.

	MEAN EGG VOLUME CATEGORIES (ml)					
	< 23.0 >		< 23.5 >		< 24.0 >	
a)						
DIED	18	19	22	17	29	10
SURVIVED	12	31	12	29	20	21
	$X^2 = 3.84$, $p<0.05$		$X^2 = 6.03$, $p<0.02$		$X^2 = 5.49$, $p<0.02$	
b)						
DIED	26	35	30	31	40	21
SURVIVED	4	15	4	15	9	10
	$X^2 = 2.87$, $P<0.10$		$X^2 = 4.67$, $P<0.05$		$X^2 = 2.04$, $P<0.20$	
c)						
DIED	8	16	8	14	11	11
SURVIVED	4	15	4	15	9	10
	$X^2 = 0.77$, NS		$X^2 = 1.06$, NS		$X^2 = 0.00$, NS	

4.3.6 Incubation period

The incubation period can only be determined accurately by finding nests during laying and visiting them at daily intervals to determine the date of laying of the last egg. Closer to hatching, the nest would again have to be visited at daily intervals to determine the hatch

date. This level of disturbance was considered to be incompatible with the main aims of this study and an alternative, but less accurate, method was used. In those nests found during laying and in which the completed clutch sizes and hatch dates were known, the date on which the last egg was layed (and, therefore, the start of incubation) was estimated by assuming that the most recent egg of the incomplete clutch had been layed on the day of finding and that the laying interval was two days between consecutive eggs. The accuracy of this method depends on these two assumptions. However, it is unlikely that the results are seriously biassed, since the incubation period of each nest was calculated in the same way and the results are intended only for purposes of comparison.

The estimated incubation periods varied between 21 and 28 days, with a mean of 25.2 (s = 1.831). There was a marked reduction in the duration of incubation with the advancement of the laying season (Fig. 4.13). This could be due either to progressive changes in egg size and quality, or to behavioural changes on the part of the incubating adults. The former is unlikely since there was no significant relationship between mean egg size and first egg date for these clutches ($r = -0.09$, $n = 15$). It is more likely that the reduction in the incubation period is due to the adults intensifying their incubation effort in later clutches. Since no information on the length or pattern of incubation shifts in nests of different laying dates is available, the validity of this hypothesis cannot be evaluated.

4.4 DISCUSSION

Certain features of avian reproduction e.g timing of breeding and clutch size, have been shown to be partly inherited (Ojanen *et al.* 1979, van Noordwijk *et al.* 1980). However, since individuals are

variable in these features between breeding attempts (Perrins and Birkhead 1983), it seems likely that they inherit predispositions which only approximate those of their parents, together with an ability to superimpose on to this an appropriate response to varying environmental and their own physiological conditions. Such variability in parental condition and habitat quality is likely to be expressed both in the two main reproductive parameters (timing of breeding, clutch size) and in egg size and quality.

Timing of breeding

Various proximate factors are known to affect the timing of laying in birds. In seasonal environments, daylength and the food supply for the laying female have been shown to be important (Murton and Westwood 1977). In this study, however, the timing of laying did not differ either between habitats (with widely different prey biomasses) or between years with markedly different rainfall and temperatures. With only three year's data it is not possible to draw firm conclusions, but it appears that the timing of laying in Lapwings is determined mainly through some constant proximate factor, e.g daylength, with weather and habitat quality having little effect. This finding conflicts with that of Hogstedt (1974) who showed that Lapwings which occupied territories with a richer food supply laid earlier. In this study, however, birds did not feed on their breeding territories but on communal areas elsewhere (Chapter 3).

Clutch size

In common with most other waders (Maclean 1972), the great majority of Lapwing clutches comprise four eggs (almost 80% of clutches). The causes of clutch size conservatism among waders are arguable but likely hypotheses invoke constraints due to the ability of the parents to protect or tend large broods (Safriel 1975, Walters 1982), or to

the optimal configuration of four pyriform eggs in minimising heat loss (Andersson 1978). Whatever the reasons, Lapwings are, apparently, limited in their ability to lay more or fewer eggs. Consequently, differences in habitat and parental quality are more likely to be expressed in egg size and quality than clutch size.

Egg size and quality and chick survival

The greatest mortality of Lapwing chicks occurred during the first few days after hatching (Chapter 5). This is a critical period for most wader chicks since they must learn to feed themselves and may have to move long distances to find suitable feeding sites. Furthermore, since the thermoregulatory capacities of very young chicks are poorly developed and they rely on the parents for frequent brooding (Norton 1973, Pienkowski 1984), cold, wet weather might limit their food intake (by depressing insect activity and by forcing the chicks to seek frequent brooding) and, ultimately, jeapordise their survival. One way in which the female parent might insure her young against such a fate is to lay larger eggs which provide them with extra reserves to sustain them during early life.

Each Lapwing egg is equivalent to approximately 11% of the female body weight so that the modal clutch size of four eggs represents about 44% of the maternal body weight. In addition, the yolks are large (Table 4.12) and the lipid content correspondingly high. These features are typical of birds with precocial young and are thought to be adaptive in that they result in eggs with high energy densities and total energy content. These are necessary to finance the advanced developmental state of the chicks at hatching and provide them with a reserve to sustain them during the first few days after hatching. Most of the energy in the egg is contained in the yolk (Carey et al. 1980), and more than 50% of the initial yolk content may

be retained by the chick at hatching (in O'Connor 1984). Large Lapwing eggs have greater yolk, lipid and, hence, energy contents; they produce bigger chicks which probably have larger yolk and/or protein reserves, and which survive better than chicks from smaller eggs. Environmental/physiological influences on egg size might, therefore, be important for chick survival and deserve some attention.

Factors affecting egg size: a) Heritability and maternal body condition. Several studies have shown that the egg size coefficient of heritability in the Domestic Fowl Gallus gallus is about 0.51, i.e approximately 50% of the observed egg size variation is due to inherited differences between females and thus susceptible to natural selection (Hill et al. 1966). By hierarchical partitioning of the variation in egg dimensions in five wader species, Vaisanen et al. (1972) showed that the components of the total variation due to laying sequence within the clutch and between laying attempts by individual females (in the same and subsequent seasons) were small. Approximately 20% of the total variation was due to differences within clutches and 60% to differences between females. Vaisanen et al. concluded that since the latter value is similar to the figure obtained by crossing experiments in the Fowl the heritable component of the variation in wader egg size was at least as high. However, by assuming that all such variation is determined genetically, this conclusion ignores the possible effect of phenotypic maternal differences on the between females component of variation.

This study has shown that Lapwings are similar to the other wader species so far studied in that most of the variability in egg size can be assigned to a between females component (about 64% of the total variation). This does not necessarily mean, however, that the coefficient of heritability is 0.64, since some of this variation

could be due to phenotypic effects. That this may be so is suggested by 36% of the between females variation being explained by differences in maternal body condition. The possible effect of genotype on body condition has not yet been investigated (the predisposition to accumulate fat or protein reserves may be more or less under genetic control). However, if body condition is purely phenotypic and a consequence of environmental factors e.g food availability, then the heritable component of the egg size variation is reduced to 41% of the total.

There is evidence that body condition may be important in determining egg size in other wader species. Vaisanen et al. (1972) claimed that female body size (i.e structural size rather than weight) had an effect on egg size. However, of the five species which they studied, in only three were there significant correlations between female measurements and egg size. In only one of these, (Dunlin Calidris alpina), was egg size correlated with some measure of female structural size (bill and wing length), while in the other two (Ringed Plover Charadrius hiaticula, and Redshank Tringa totanus) only maternal weight was significantly correlated with egg size. The remaining two species: Temmincks Stint Calidris temminckii and Red-necked Phalarope Phalaropus lobatus are atypical in that the former lays two clutches per season while the latter is polyandrous with the male undertaking all of the incubation. In both, the correlations between female weight and egg size were negative (though not significantly so). This suggests that some special relationship exists between female weight and egg size, presumably as a result of their unusual mating systems (perhaps heavier females are more likely to be double brooded but must lay lighter eggs to do so).

These results indicate that although egg size in waders is likely to be genetically determined, the extent of genotypic influence

may not be as great as claimed by Vaisanen et al. (1972). Phenotypic influences may also be important and more accurate estimates of the heritability coefficient will be made only when the relationship between genotype, environment and adult body condition is understood.

b) Clutch size, habitat and clutch number. Eggs in clutches of two on the arable site were significantly smaller than those in larger clutches. The reasons for this size difference are not known but may involve maternal age or body condition. Age effects on egg size have been previously noted in seabirds (e.g Coulson 1963, Furness 1983) and in one study of Charadriids (Gratto et al. 1983). Since, however, clutches of two eggs comprised less than 5% of all arable clutches (Table 4.1), this effect is unlikely to have important consequences for population dynamics.

Eggs on the rough grazing study area were generally smaller than those on the arable site (Table 4.9). This was found in both first and replacement clutches but the difference was greatest in the latter because females on the rough grazing site tended to lay smaller eggs in their replacement clutches. This might indicate that the factors causing size differences in the earlier clutches are accentuated later in the season. It could be due either to a reduction in the availability of food (earthworms burrow deeper in the summer (Edwards and Lofty 1972) and may become inaccessible), or to a progressive deterioration in maternal body condition due to poorer feeding.

Possible habitat differences in Lapwing egg sizes have been previously noted by Murton and Westwood (1974), who showed that birds nesting on Cambridgeshire arable farmland laid heavier eggs than birds on East Anglian Breckland. This difference was attributed to the greater densities of earthworms available to the laying females on arable farmland. Unfortunately, however, the stage of incubation was

not ascertained and the observed differences in egg weight could have been due simply to different degrees of water loss. Further evidence that food limitation might be important for Lapwings was provided by Hogstedt (1974) who showed that females laid earlier in territories which were richer in earthworms. This was presumably because they were able to form their eggs more quickly.

Habitat quality (in terms of the food available to the adults) has an indirect effect on the quality and survival of Lapwing chicks. Egg size is at least partly determined by maternal body condition, which is likely to be dependent on food availability (Chapter 3). On the rough grazing site food availability and adult feeding success (Chapter 3) and maternal body condition were all poor in comparison to the arable study area. These factors are likely to be at least partly responsible for the smaller eggs on the rough grazing site. On the arable study area the food supply was richer, feeding success higher and maternal condition better. This resulted in bigger eggs and, if all other things had been equal, should have enhanced chick survival. Unfortunately, however, any advantages to hatching from the larger eggs on the arable site were normally outweighed by a high chick mortality due to anthropogenic factors (Chapter 5).

Figure 4.1

Reduction in mean egg density with stage of incubation. Open and closed symbols = arable and rough grazing respectively.

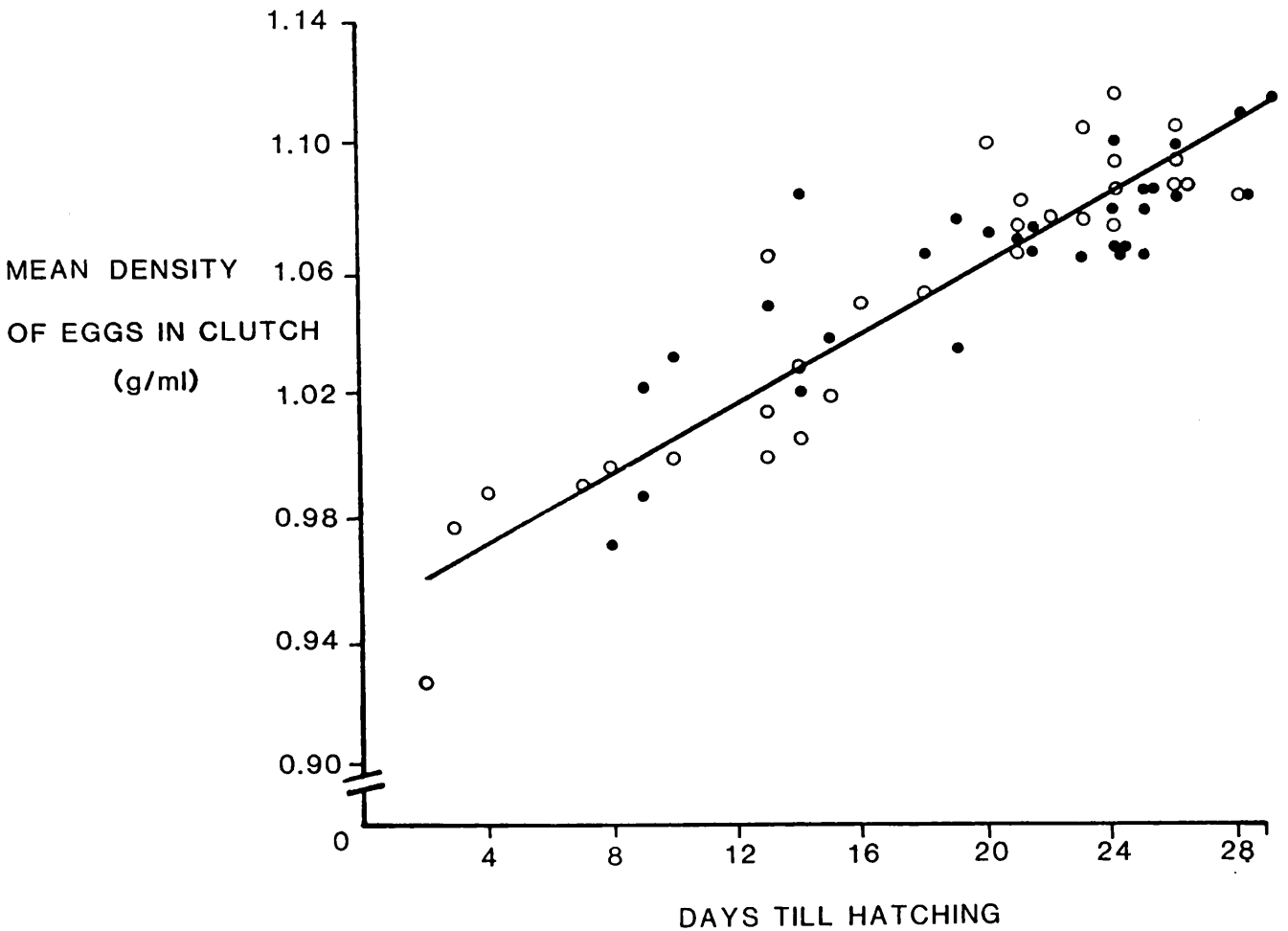

MEAN DENSITY
OF EGGS IN CLUTCH
(g/ml)
1.14
1.10
1.06
1.02
0.98
0.94
0.90
0
4
8
12
16
20
24
28
DAYS TILL HATCHING

Figure 4.2

Distribution of first egg dates in 154 rough grazing and 135 arable clutches in 1984 and 1985. The hatched area denotes clutches in arable fields which were cultivated abnormally late in the spring.

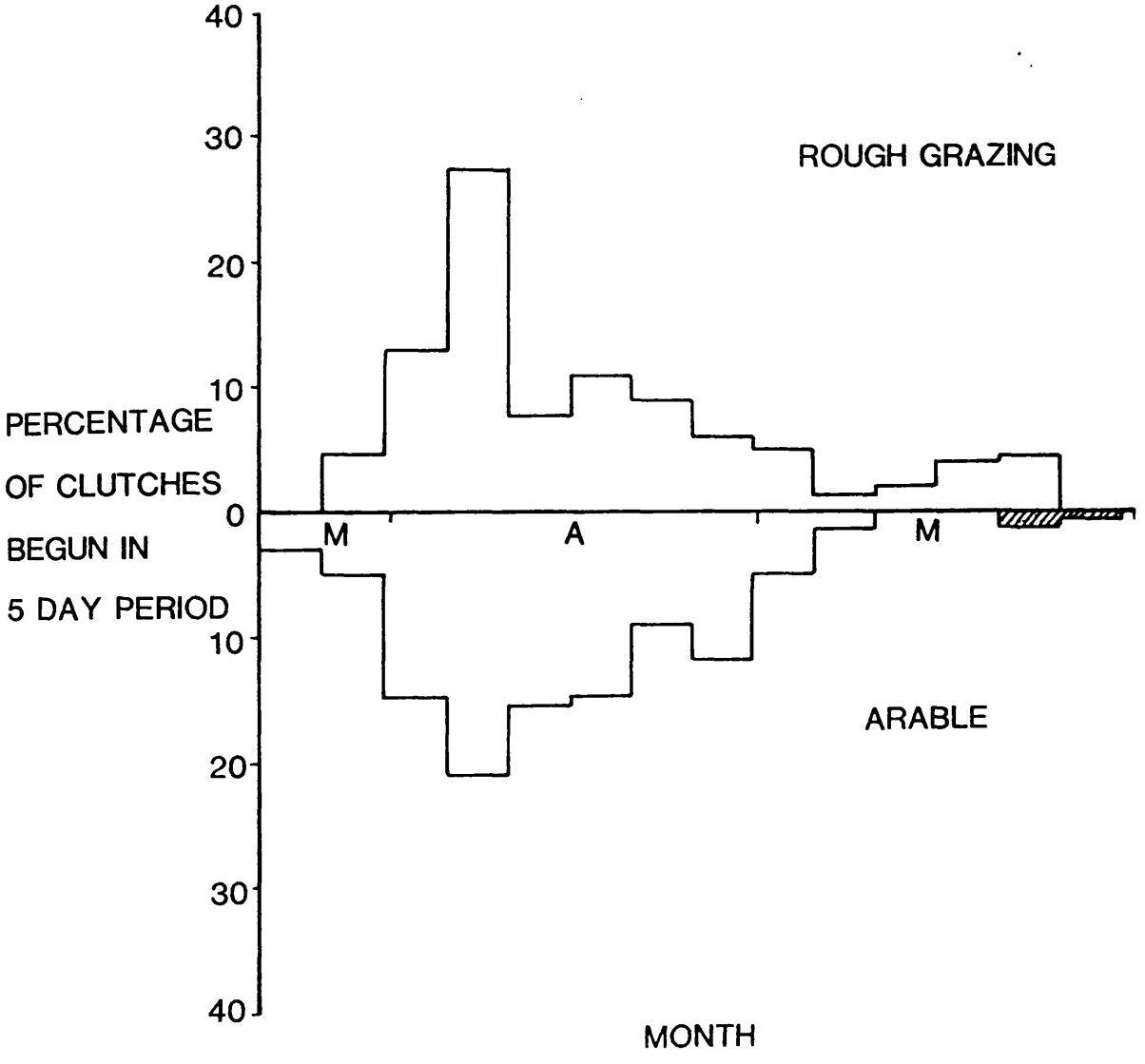
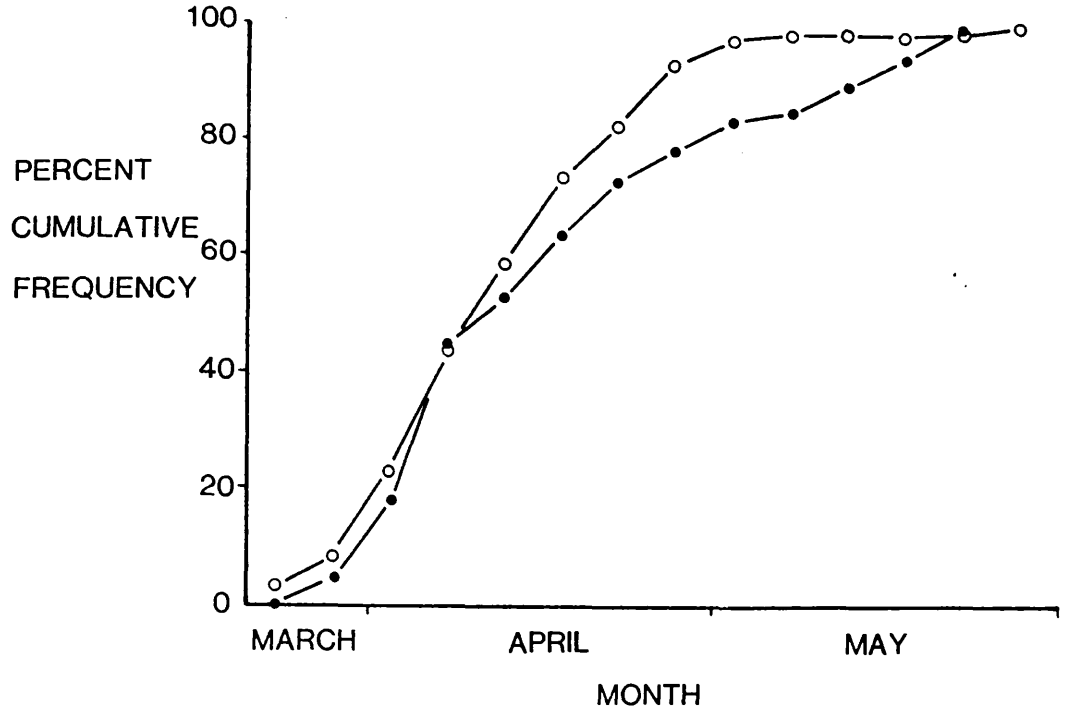

40
30
20
10
0
10
20
30
40
PERCENTAGE
OF CLUTCHES
BEGUN IN
5 DAY PERIOD
M
A
M
ROUGH GRAZING
ARABLE
MONTH

Figure 4.3 (upper).

Cumulative percent frequency curves of first egg dates in 154 rough grazing (solid symbols) and 135 arable (open symbols) clutches.

Figure 4.4

Cumulative percent frequency curves of first egg dates on the rough grazing site. Solid circles = 1984 (n = 67); open circles = 1985 (n = 54); squares = 1986 (n = 33).


100
80
60
40
20
0
PERCENT
CUMULATIVE
FREQUENCY
MARCH
APRIL
MAY
MONTH

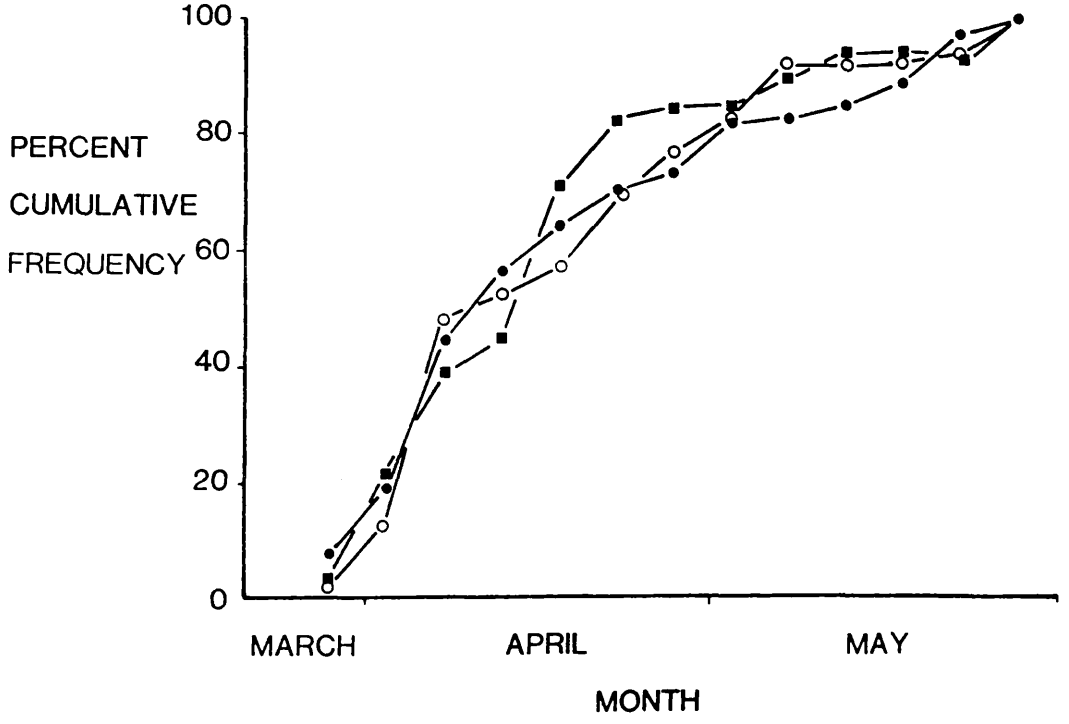

100
80
60
40
20
0
PERCENT
CUMULATIVE
FREQUENCY
MARCH
APRIL
MAY
MONTH

Figure 4.5

Mean daily air temperature (recorded at 0900 hrs GMT and 1m above ground level) and the cumulative percentage of clutches begun in both study areas in each five day period between March and April. Solid symbols = cumulative percent, open symbols = air temperature.

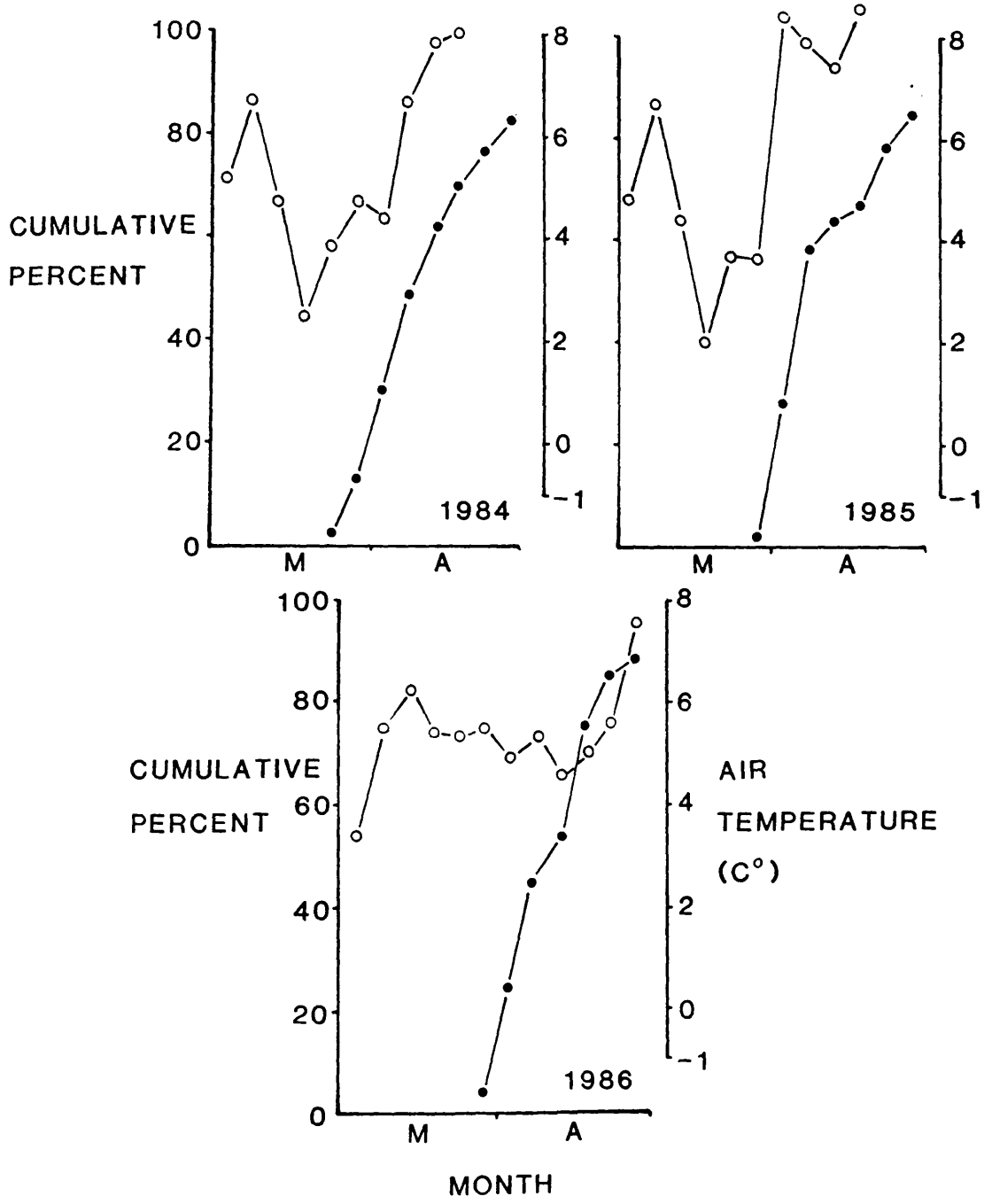
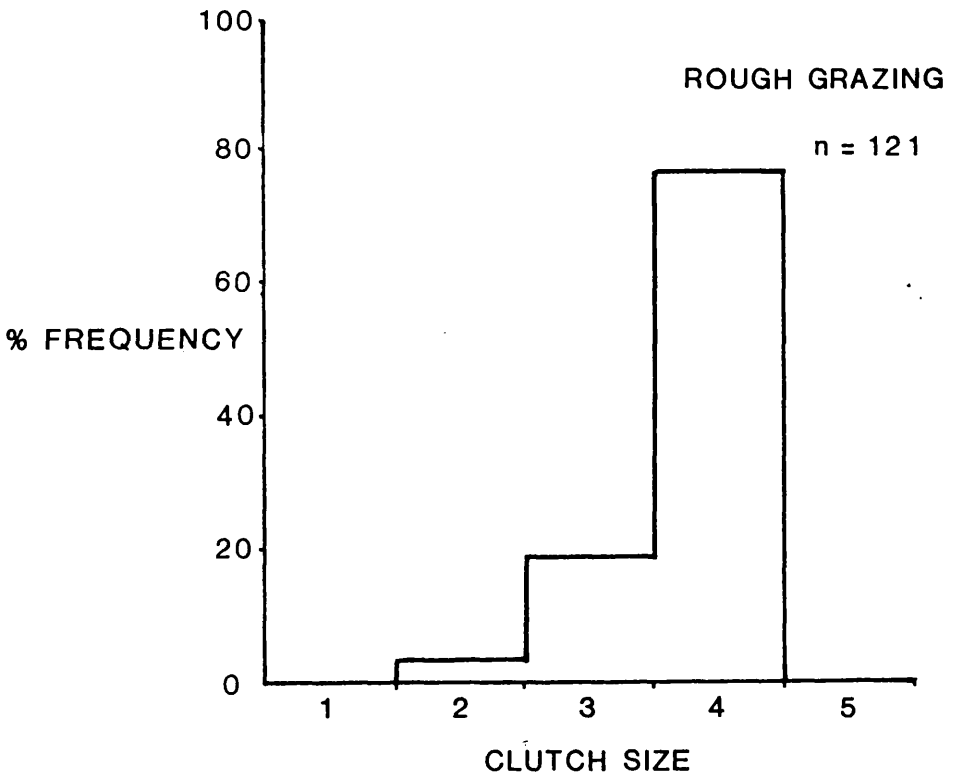

CUMULATIVE
PERCENT
100
80
40
20
0
8
6
4
2
0
-1
1984
1985
1986
M
A
CUMULATIVE
PERCENT
60
AIR
TEMPERATURE
(C°)
MONTH

Figure 4.6

Percentage frequency of different clutch sizes in the two study areas. Clutches begun on spring cereal fields before 10th April are excluded from the arable sample because of the possibility of disturbance affecting clutch size (see text and Table 4.4).


ROUGH GRAZING
n = 121
% FREQUENCY
100
80
60
40
20
0
1
2
3
4
5
CLUTCH SIZE

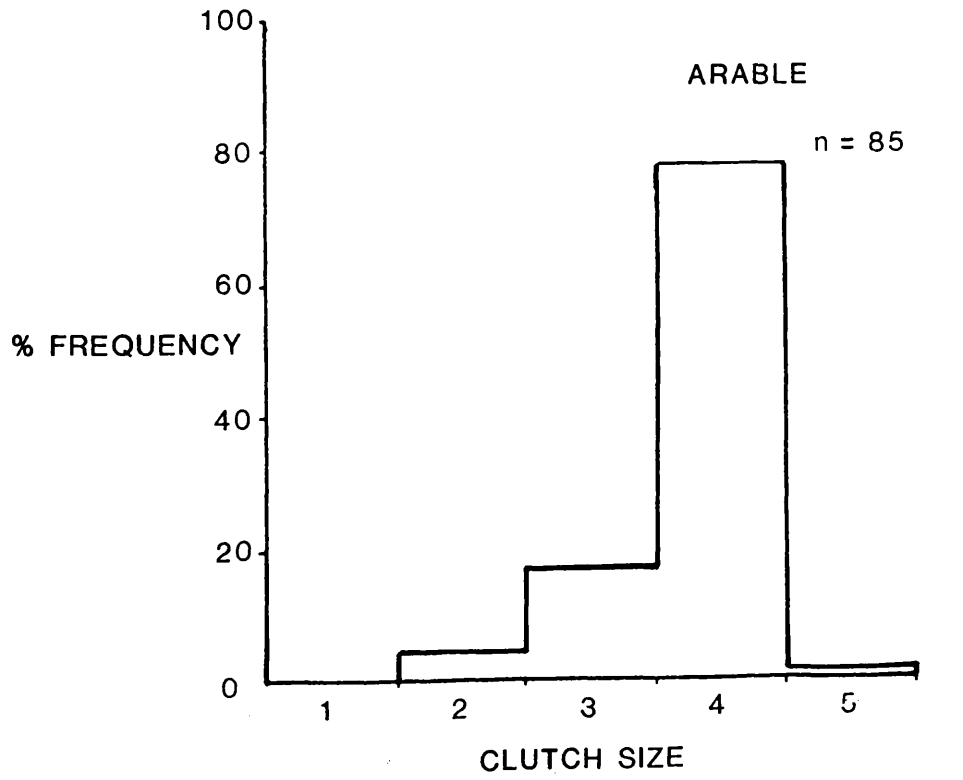

ARABLE
n = 85
% FREQUENCY
100
80
60
40
20
0
1
2
3
4
5
CLUTCH SIZE

Figure 4.7

Percent frequency distributions of: a) individual egg volumes and, b) mean egg volumes within clutches in both study areas. Upper = rough grazing, lower = arable.

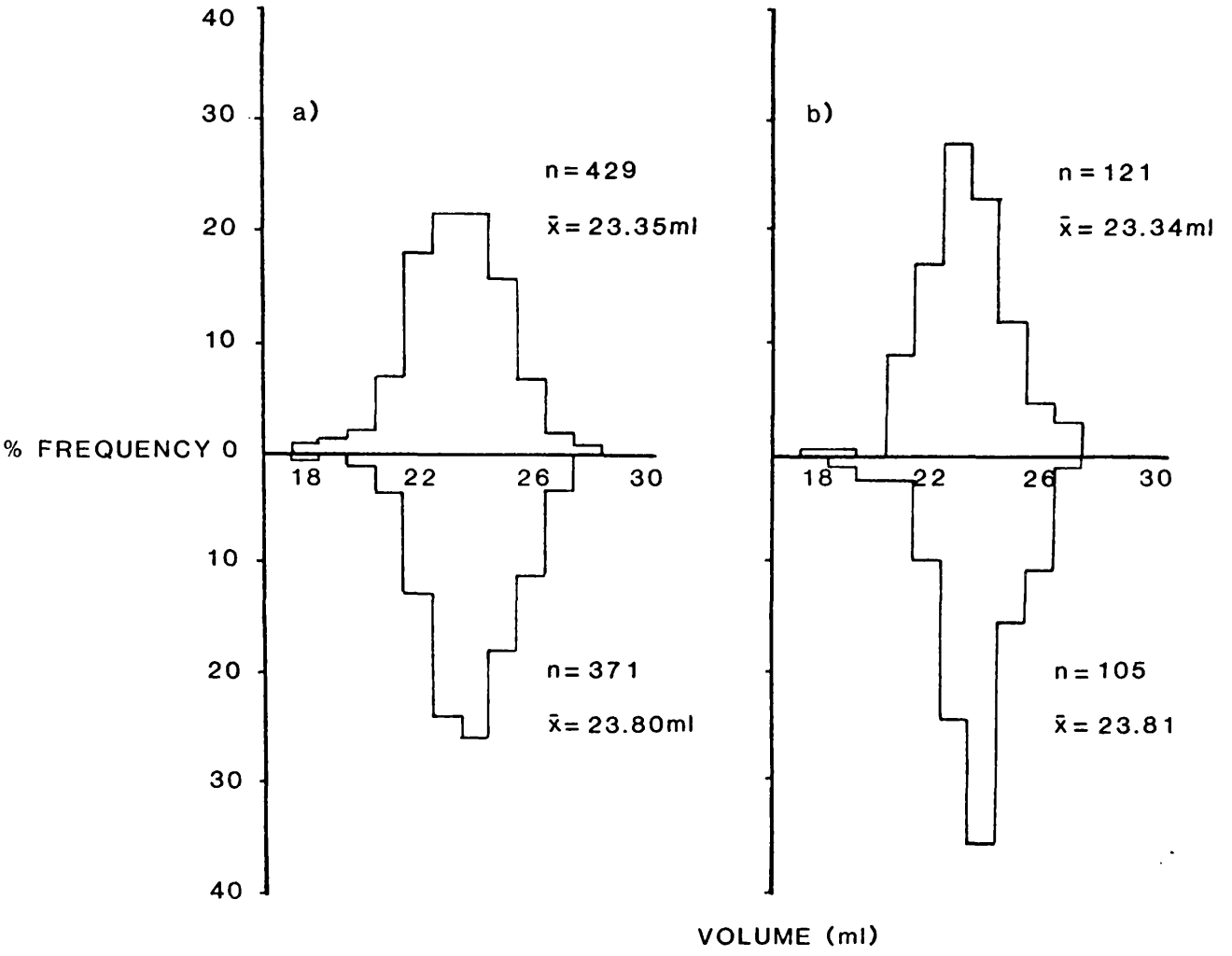

40
30
20
10
0
10
20
30
40
% FREQUENCY
a)
n = 429
x̄ = 23.35ml
n = 371
x̄ = 23.80ml
b)
n = 121
x̄ = 23.34ml
n = 105
x̄ = 23.81
18
22
26
30
VOLUME (ml)

Figure 4.8

Relationship between the body condition (weight/wing length) of 18 incubating female Lapwings and the mean egg volumes in their clutches.

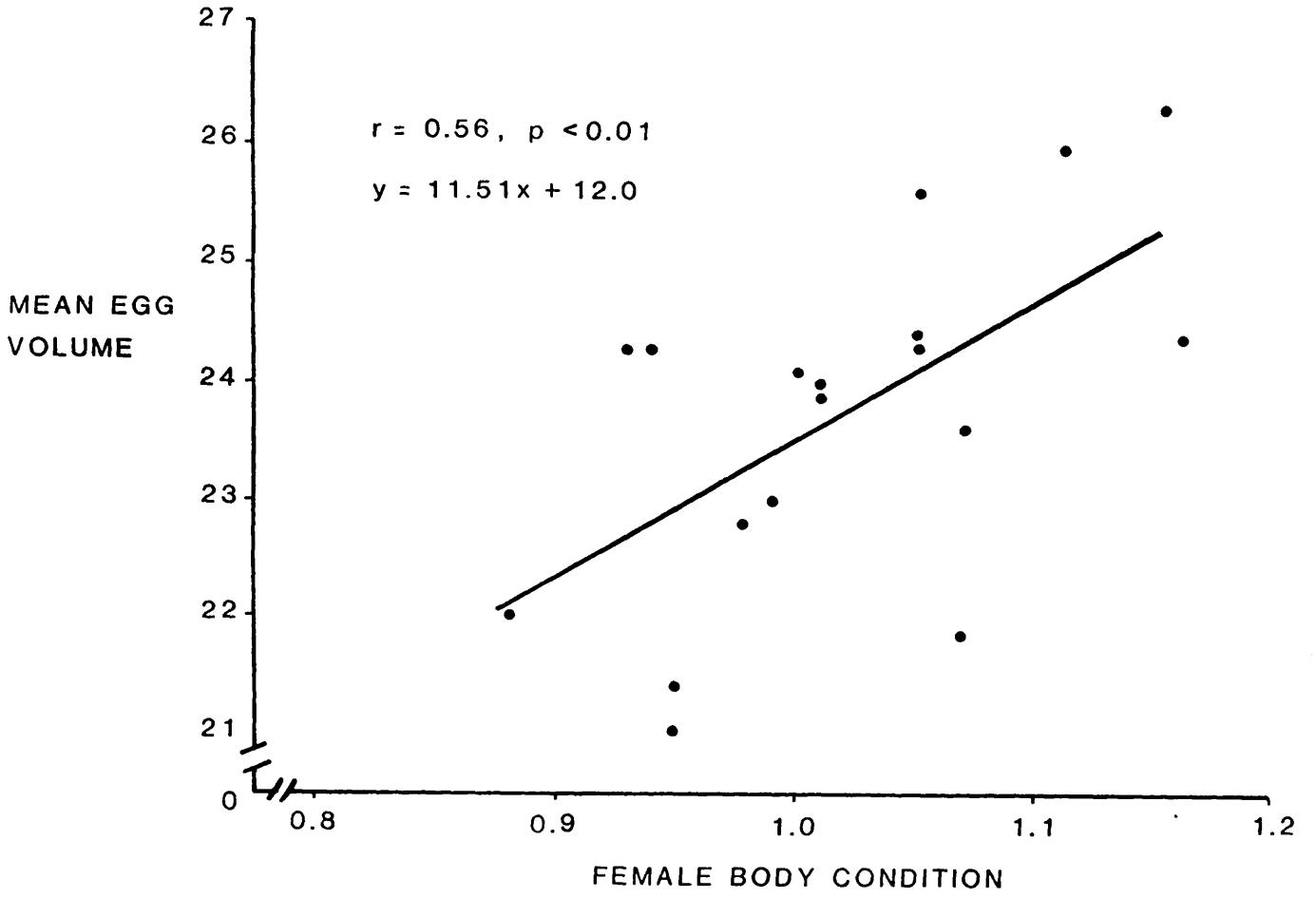

r = 0.56, p <0.01
y = 11.51x + 12.0
MEAN EGG VOLUME
27
26
25
24
23
22
21
0
0.8
0.9
1.0
1.1
1.2
FEMALE BODY CONDITION

Figure 4.9

Relationship between egg shape (length/breadth) and volume. Vertical bars = plus and minus 1 s.d.

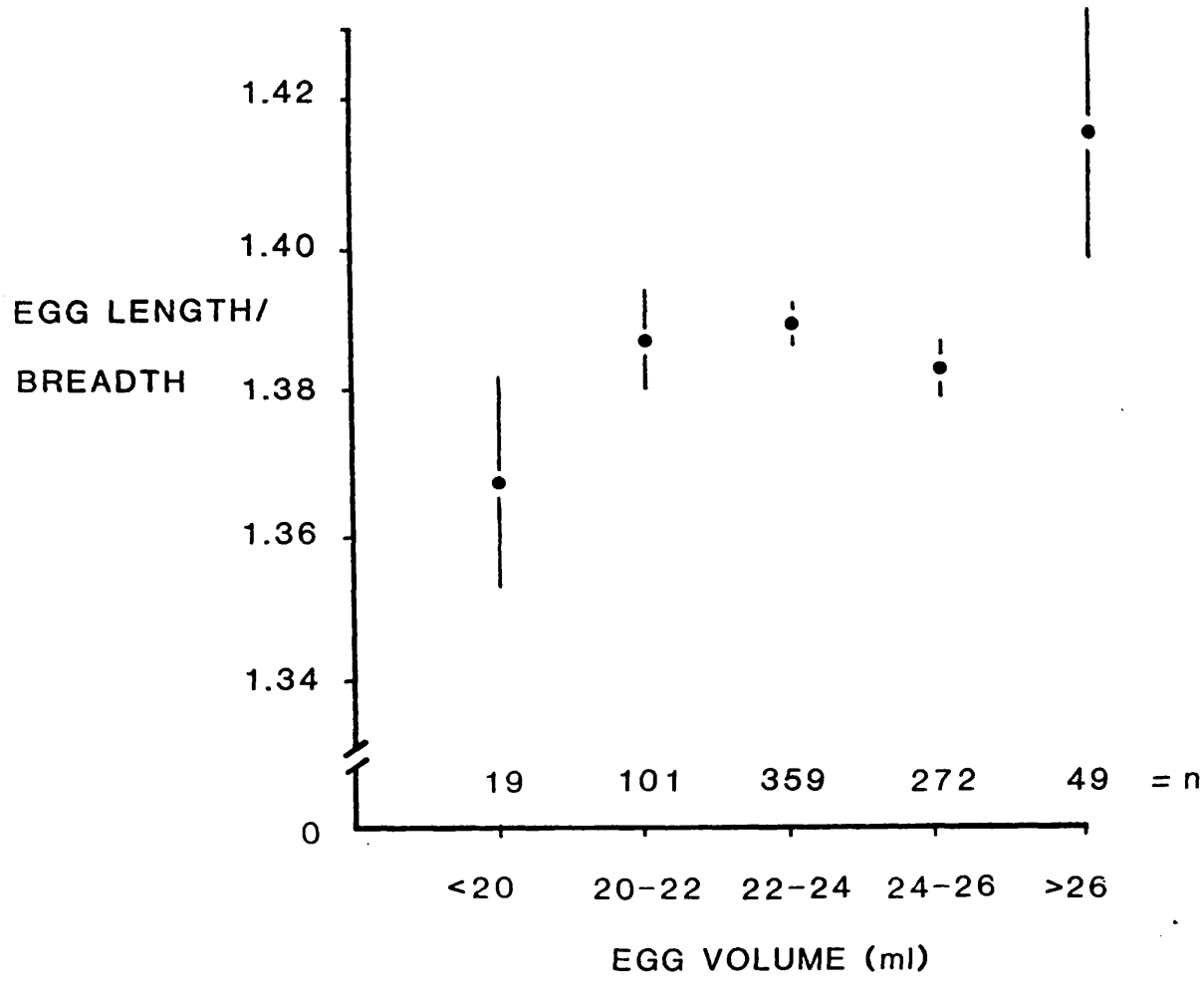

1.42
1.40
EGG LENGTH/
BREADTH
1.38
1.36
1.34
0
19
101
359
272
49
= n
<20
20-22
22-24
24-26
>26
EGG VOLUME (ml)

Figure 4.10

Change in percentage composition of Lapwing eggs with increasing size. Lines calculated from slopes and intercepts in Table 4. 14.

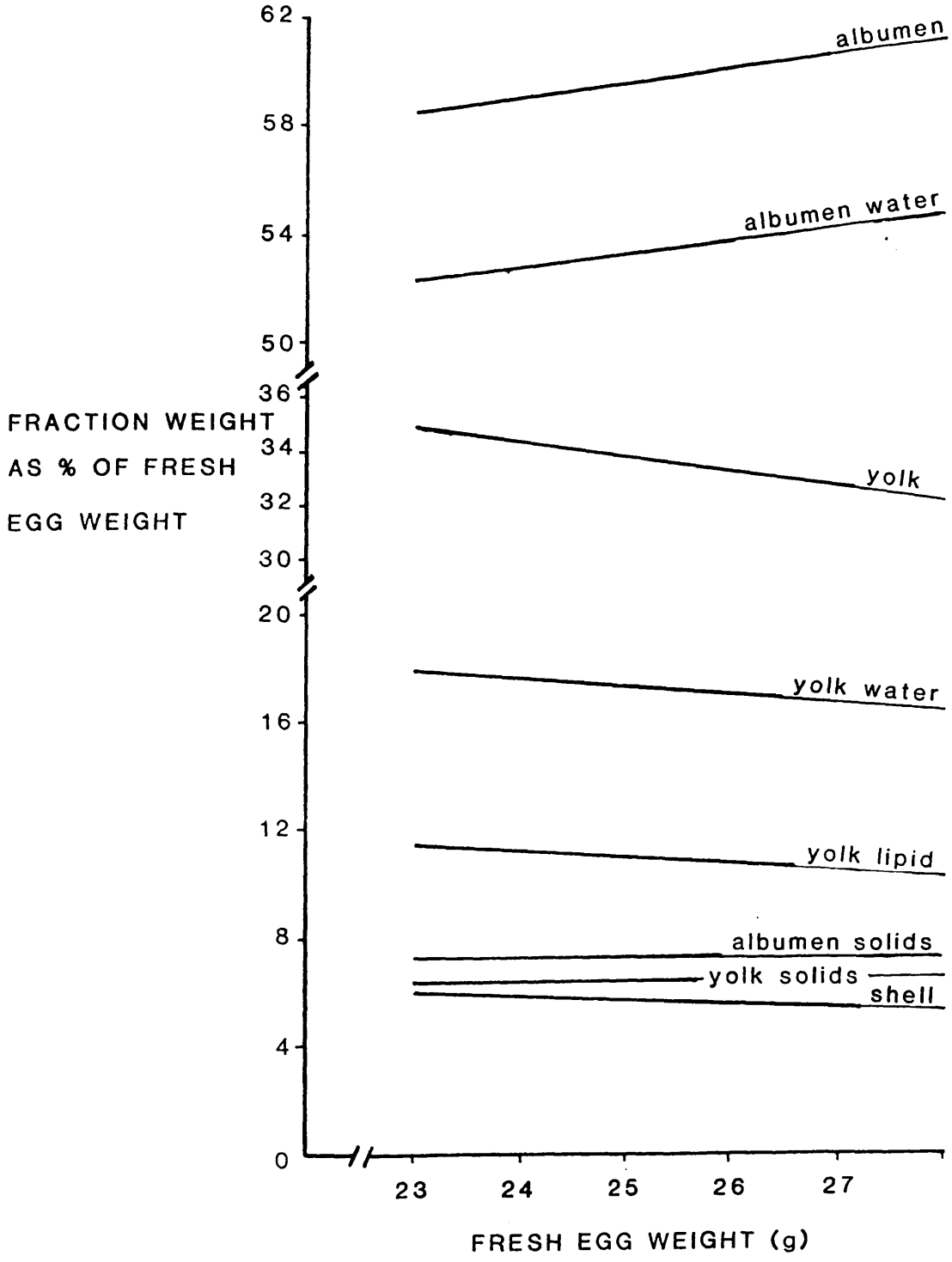

62
58
54
50
36
34
32
30
20
16
12
8
4
0
FRACTION WEIGHT
AS % OF FRESH
EGG WEIGHT
albumen
albumen water
yolk
yolk water
yolk lipid
albumen solids
yolk solids
shell
23
24
25
26
27
FRESH EGG WEIGHT (g)

Figure 4.11

Relationship between the weights of hatchlings (i.e chicks in the nest and still wet from hatching) and the mean egg volume of the clutch from which they hatched.

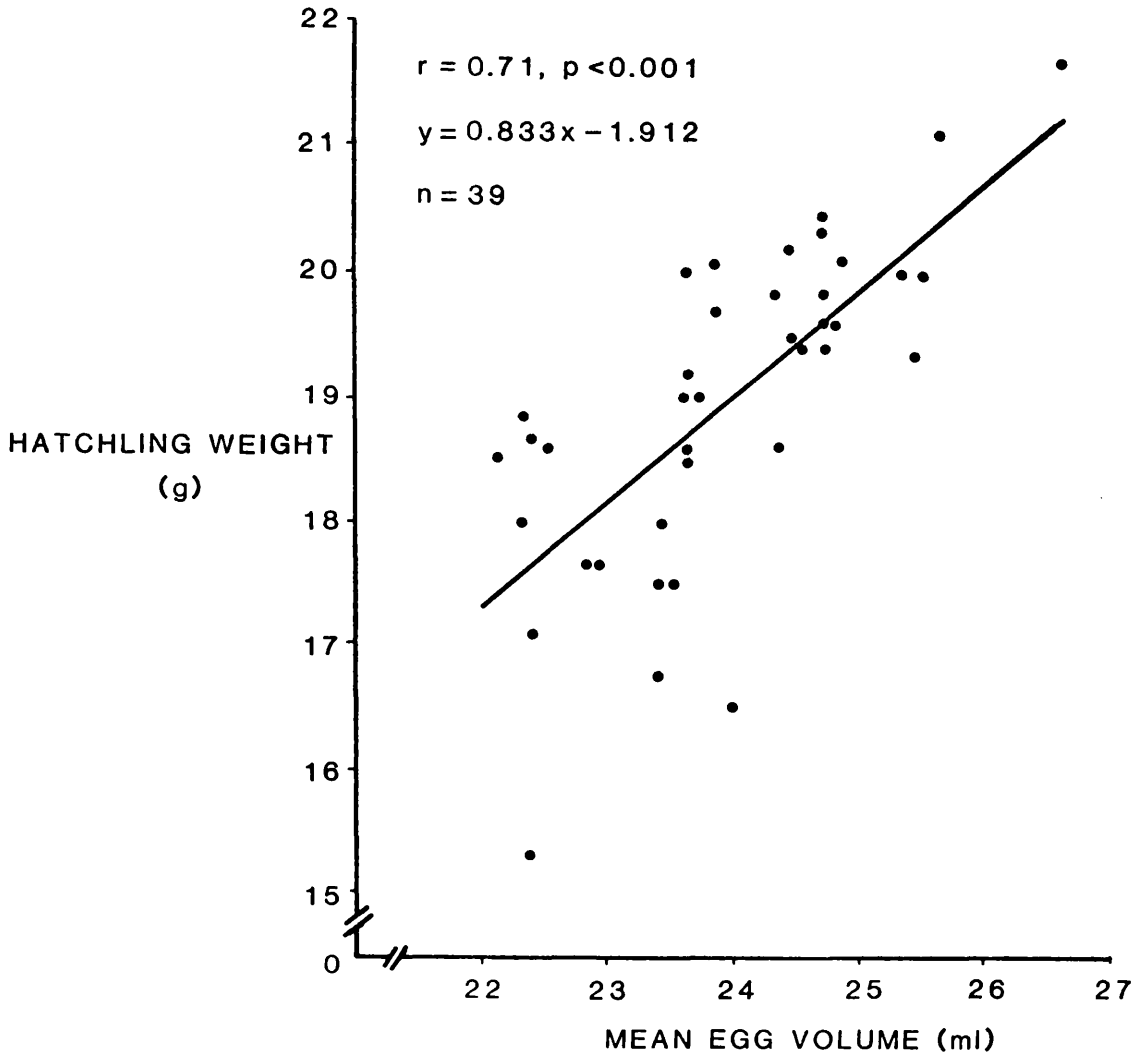

r = 0.71, p <0.001
y = 0.833x – 1.912
n = 39
HATCHLING WEIGHT (g)
22
21
20
19
18
17
16
15
0
22
23
24
25
26
27
MEAN EGG VOLUME (ml)

Figure 4.12

Fledging success of Lapwing chicks in relation to the mean egg volumes of the clutches from which they hatched.

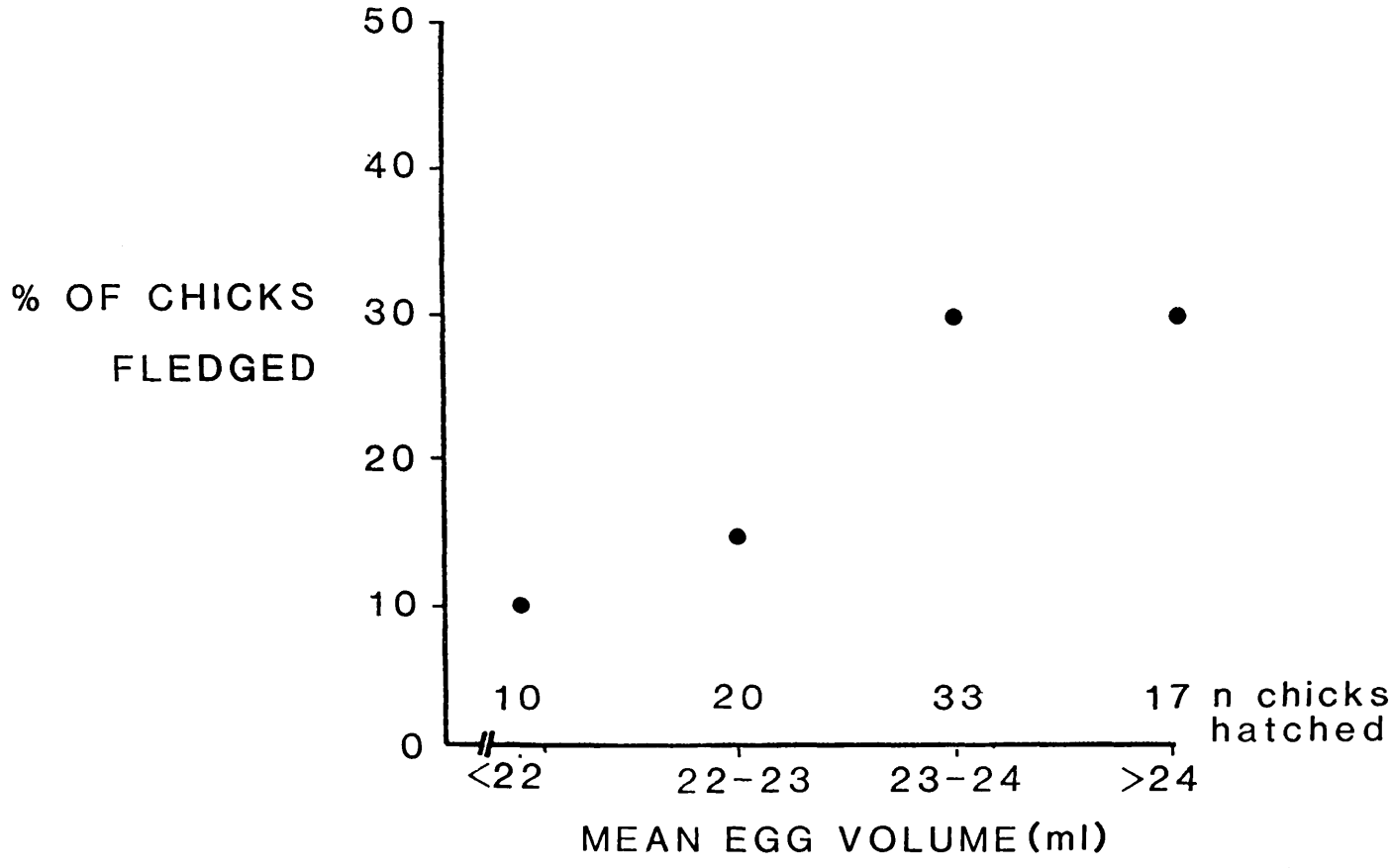
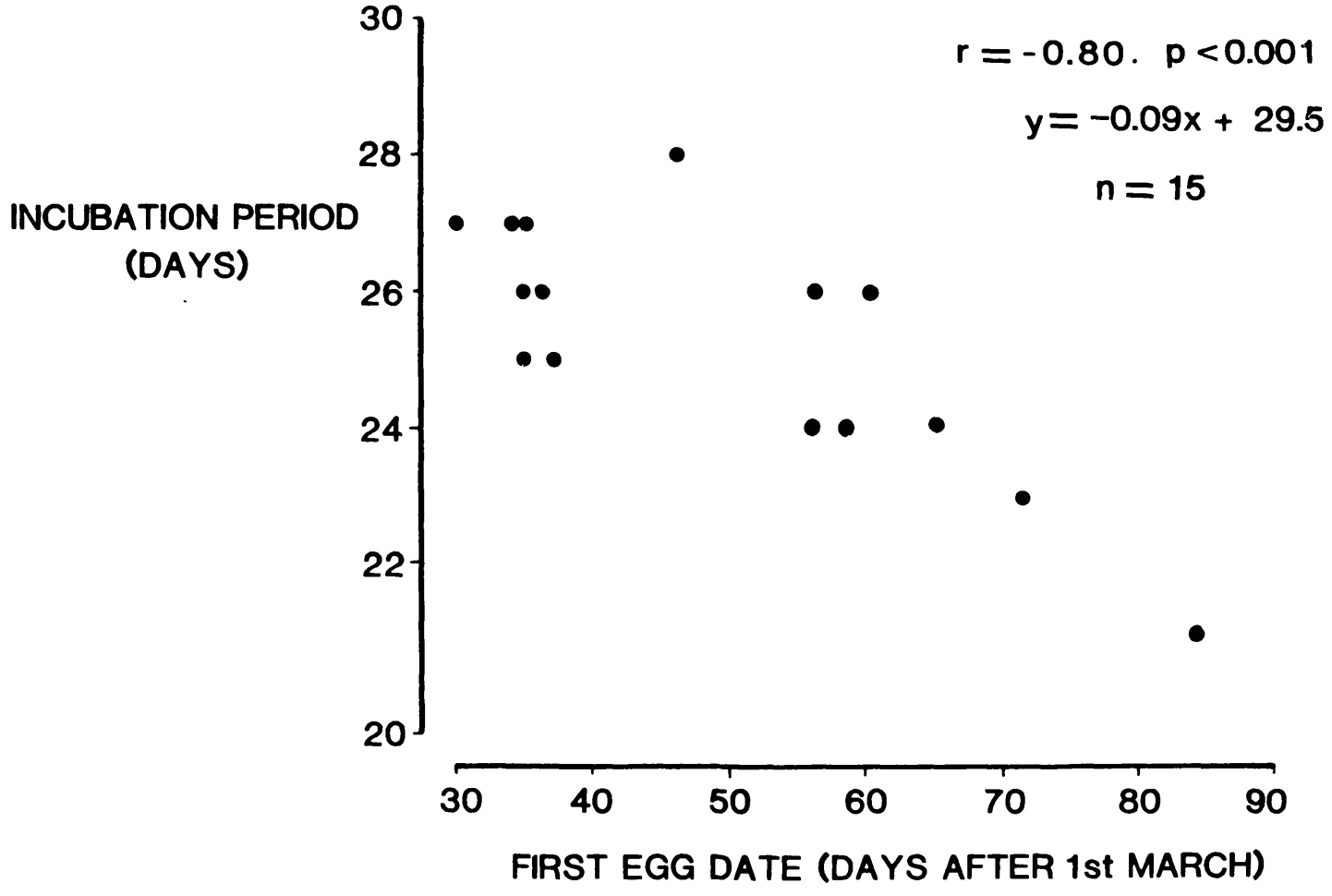

% OF CHICKS FLEDGED
50
40
30
20
10
0
10
20
33
17 n chicks hatched
<22
22-23
23-24
>24
MEAN EGG VOLUME (ml)

Figure 4.13

Duration of incubation period in relation to the date of laying of the first egg.


r = -0.80. p < 0.001
y = −0.09x + 29.5
n = 15
INCUBATION PERIOD (DAYS)
30
28
26
24
22
20
30
40
50
60
70
80
90
FIRST EGG DATE (DAYS AFTER 1st MARCH)

CHAPTER 5. BREEDING SUCCESS AND PRODUCTIVITY

5.1 INTRODUCTION

Avian reproductive rates are determined by a variety of factors including clutch size, number of broods raised per year, and hatching and fledging success. Among many waders the situation is simpler since they display comparatively little clutch size variation and raise a maximum of one brood per year. Consequently, spatial and temporal differences in productivity are largely due to variability in only two factors, hatching and fledging success. Unfortunately, this does not result in waders being easy subjects for the investigation of reproductive rates. This is mainly because the estimation of fledging success among wader chicks can be extremely difficult. There are three reasons for this difficulty: 1) wader broods can be hard to locate since they may wander widely after hatching. 2) both the adults and chicks can be highly cryptic in appearance and behaviour, making their location and the estimation of brood sizes difficult. This is particularly so in species which inhabit longer vegetation such as Snipes. 3) even when the study broods have been found, it can be difficult to determine brood size accurately because the chicks may feed some distance from the adults and each other. This becomes more of a problem as the chicks approach fledging and become more independent of their parents. For these reasons, few satisfactory studies of wader fledging success and productivity have been reported, although hatching success estimates are more plentiful.

Wader hatching success varies widely both inter- and intra-specifically (Table 5.1). The reasons for this variability have been shown to include disturbance by humans (Pienkowski 1984b), mortality of eggs and incubating adults during freak storms (Graul 1975, Grover and Knopf 1982), inundation by high tides (Hale 1980), the nesting

density and group mobbing behaviour of conspecifics and other waders (Drycz et al. 1981), and infertility and accidental damage to eggs during incubation (Evans and Pienkowski 1984). In most studies, however, the greatest egg losses have been reported as due to natural predators, and intra-specific variability in hatching success attributable largely to differences in predator density and hunting behaviour (Byrkejedal 1980, Meltofte et al. 1981, Pienkowski 1984b, Wiens and Cuthbert 1984).

Table 5.1. Hatching success (% of eggs hatching) among European waders.

SPECIES	LOCALITY	HATCHING SUCCESS	AUTHORITY
OYSTERCATCHER	ENGLAND	18 - 53	BRIGGS (1984)
"	WALES	44 - 82	HARRIS (1967)
"	SCOTLAND	25 - 68	HEPPLESTON (1972)
RINGED PLOVER	ENGLAND	1 - 43	PIENKOWSKI (1984)
REDSHANK	ENGLAND	18 - 48	HALE (1980)
DUNLIN	FINLAND	55 - 84	SOIKELLI (1967)

Fledging success is also highly variable among waders (Table 5.2). The reasons for these differences are similar to those responsible for hatching success variability, except that starvation, either due to food shortage or to other factors, for example bad weather reducing the time available for feeding (Meltofte 1976), may also be important. The few productivity estimates that have been made vary from 0.1 - 1.0 fledged chicks/pair in Oystercatchers (Heppleston 1972, Briggs 1984), 1.7 - 2.1 fledged chicks/pair in the Piping Plover Charadrius melodus (Weins and Cuthbert 1984), and 0.8 fledged chicks/pair in the Stone Curlew Burhinus oedicnemus (Westwood 1983).

Table 5.2. Fledging success (% of chicks surviving to fledging) among chicks of European waders.

SPECIES	LOCALITY	FLEDGING SUCCESS	AUTHORITY
OYSTERCATCHER	GERMANY	5	DIRCKSEN (1932)
"	WALES	86	KEIGHLEY (1949)
"	SCOTLAND	27 - 46	HEPPLESTON (1972)
"	ENGLAND	67 - 77	BRIGGS (1984)
RINGED PLOVER	ENGLAND	45	PIENKOWSKI (1984)
KENTISH PLOVER	GERMANY	50	RITTINGHAUSE (1956)
STONE CURLEW	ENGLAND	39	WESTWOOD (1983)

Most wader chick mortality has been reported as occurring in the first few days after hatching. This is a period when their feeding efficiency is likely to be low and, since they are unable to thermoregulate properly (Chappel 1980), they may be most vulnerable to the effects of weather (e.g Pienkowski 1984, Heppleston 1972, Soikelli 1970). Previous studies of lapwing breeding biology have shown that predation and weather can have important effects on hatching and fledging success. In Germany hatching success varied between 11 and 94% but was highest in years when predators were less abundant (Kooiker 1984). Fledging success among lapwings breeding on an abandoned airfield in southern England was comparatively high during cool, wet weather (Jackson and Jackson 1980). This was because human disturbance was a major determinant of breeding success and it was least intense in poorer weather.

Agricultural influences on breeding success have also been found in waders (Beintema et al. 1985), and among Lapwings in particular (Beser and Helden-Sarnowski 1982, Matter 1982, Kooiker 1984). These have been due to clutch destruction during soil cultivation, trampling

by stock, crushing by farm machinery, or starvation. In contrast, Briggs (1984) found that by breeding on undisturbed pasture, hay or silage fields, Oystercatchers were able to increase their hatching success above that of birds breeding in coastal or adjacent riparian habitats.

The consequences of nesting on farmland are likely to vary between species depending on their morphology and breeding behaviour relative to the agricultural regime, i.e the extent of their adaptation to their particular agricultural habitat. Timing of breeding, feeding and nest-site requirements in relation to cultivation regime, crop type and growth, and whether the young feed themselves or are fed by the adults may all be important. In this chapter Lapwing breeding success and productivity in different agricultural habitats are compared. The factors responsible for inter- and intra-habitat differences are investigated, and the implications of farmland nesting for long-term population stability are discussed.

5.2 METHODS

5.2.1. Hatching success

Clutch survival was investigated using the technique developed by Mayfield (1961 and 1975). The simplest method of expressing hatching success involves dividing the number of nests that successfully hatched one or more chicks by the total number of nests in the sample, and then multiplying by 100 to give percent hatching success. However, since this method does not take account of those nests which failed before they could be found, it may overestimate actual hatching success (Snow 1955). Mayfield's method overcomes this difficulty by calculating a daily rate of nest loss among the nests which were found, and by assuming that a similar rate applies to those nests lost before finding. Loss rate per day = known number of nests lost / total

nest-days. The daily survival probability (p) = 1 - daily loss rate, and the probability that a nest will survive to hatching (ignoring partial losses) is this figure raised to a power equivalent to the total number of days during which the nest is at risk (i.e laying + incubation periods). An unbiased estimate of hatching success (the percentage of nests which hatched one or more eggs) is then obtained by multiplying this latter result by 100. Hensler and Nicholls (1981) showed that the Mayfield estimator is, in fact, a maximum likelihood estimator and provided equations for calculating confidence limits and significance levels for daily nest survival.

An assumption of the Mayfield method is that the nest mortality rate is constant throughout the period during which the nest is vulnerable, i.e during the laying period and at all stages of incubation (Willis 1981). In this study, too few Lapwing nests were found prior to clutch completion to investigate the loss rate during laying. However, the rate of loss during incubation was constant (Fig. 5.1). For the purposes of investigating hatching success it has been assumed that clutch survival during laying and incubation did not differ.

Another potential bias in the estimation of hatching success is due to observer interference leading to an increased likelihood of predation (Hammond and Forward 1956, Picozzi 1975). It has already been shown (Chapter 2) that marking nests with short lengths of cane at distances of 20m or more did not affect subsequent survival. However, repeated visits to nests to check their contents might have aided predators by providing visual or scent clues to the nest position (cf Willis 1973). This possibility was investigated by categorising nests which were predated or which were still extant, according to their treatment on the preceeding visit (i.e scanned from a vehicle on a nearby road - sitting adults giving proof of continued

nest survival; nest approached on foot and adult flushed but eggs not handled; nest approached on foot, adult flushed and eggs handled). There were no significant differences between the fates of nests which previously had been checked using either of the above methods (Table 5.3). Nest status was usually checked from a distance without interupting incubation. However, Table 5.3 shows that even when this was not possible, visiting nests and handling the eggs did not significantly affect their survival.

Table 5.3. Condition of nests relative to the method of checking used on the previous visit. Scanning involved observing the nest from a distance (usually from within a vehicle) without disturbing the sitting adult.

METHOD	n OF OF NESTS	CONDITION ON NEXT VISIT EXTANT(%)	PREDATED(%)
SCANNED	185	171(92.4)	14(7.6)
VISITED (EGGS NOT HANDLED)	65	60(92.4)	5(7.6)
VISITED (EGGS HANDLED)	136	123(90.5)	13(9.5)

$X^2 = 0.43$, 2 d.f., ns

In a small number of failed nesting attempts it was not obvious from the behaviour of the adults whether the eggs had been predated in the final day or two of incubation or the chicks lost soon after hatching. Fortunately, this problem could be resolved by examining the condition of the nest cup. The lining of nests which had successfully hatched one or more chicks invariably contained small broken fragments of egg-shell, a feature previously noted in other wader studies (e.g Nethersole-Thompson and Nethersole-Thompson 1942, Higgins and Kirsch 1975). Predated nests did not show this feature.

5.2.2. Fledging success and productivity

Fledging success and productivity were investigated using only the clutches and broods of adults which were either artificially individually marked by colour rings and/or dye, or which were individually recognisable by virtue of peculiar plumage characteristics. Lapwings show much variability in face pattern and crest length (over and above that due to sexual dimorphism) and it was possible to identify a number of individuals using combinations of these features. During the second and third years of the study an increased emphasis was placed on artificially marking birds.

On hatching, the chicks in the study broods were marked using individually numbered metal rings and temporary leg flags in brood-specific colours (coloured PVC tape wound round the numbered metal ring), and their location and survival checked at 2-3 day intervals. To minimise disturbance, these checks were carried out either from a vehicle or from a hide. On locating a study brood, my technique was simply to observe it, without disturbing it, until I was confident that my estimate of brood size was accurate (this normally took less than 30 minutes but, under difficult circumstances, could take up to 2 hours). Determination of brood size was relatively easy when the chicks were small since they generally stay close to the adults and are brooded periodically, but was more problematic in broods of older chicks which may wander further from the adults and are, therefore, more difficult to locate. In spite of this difficulty, the method seemed to work well since there were few occasions when I had to revise my estimate of brood size upwards after subsequent checks.

Productivity is expressed as the number of chicks fledged per female. This is considered more appropriate than fledglings/pair since Lapwings may be polygynous.

5.3 RESULTS

5.3.1. Factors affecting hatching success

Although most egg losses were due either to predation or to farming operations (Table 5.4), the incidence of these factors varied seasonally and between study sites (see below). Comparatively few eggs which survived the incubation period failed to hatch due to infertility or embryo death (Table 5.4).

Table 5.4. Causes of egg failure on the arable and rough grazing study areas (all years combined). "Other" includes trampling by stock and damaged during handling.

	EGGS FAILED	PERCENTAGE OF FAILURES DUE TO: PREDATION	CULTIVATION	INFERTILITY/ EMBRYO DEATH	OTHER
ARABLE	273	59.3	29.7	7.6	3.4
ROUGH GRAZING	293	89.4	0.0	5.4	5.2

Habitat and laying date.

Although the differences were not significant, hatching success on the arable study area was lower than on the rough grazing study area in two seasons and higher in one (Table 5.5). Observations made during the course of the study suggested that hatching success among earlier clutches on the arable site may have been reduced by losses sustained during the cultivation of spring cereal fields (the preferred nesting habitat). This was investigated, initially, by separating the arable clutches into those on spring cereals or hay and comparing their daily survival probabilities (Table 5.6). Clutches in spring cereal fields had a significantly lower survival probability than hayfield clutches (Table 5.6). Cultivation on the arable site was normally completed by mid-April and when the spring cereal and rough grazing clutches were further subdivided by first egg date into two time periods, clutches

begun on and before, or after 15th April, the earlier spring cereal clutches had a significantly reduced survival probability (Table 5.7; t-test comparing early and late spring cereal clutches: $t = 4.95$, $p<0.01$). Hatching success on the rough grazing site showed no such trend with laying date (Table 5.7). When this operation was repeated but with all clutches known to have been lost due to cultivation excluded, the difference in nest survival in clutches begun before or on 15th April was reduced and was no longer significant (rough grazing = 35.3%, spring cereals = 22.0%, $t = 1.50$, ns). Thus, the cultivation regime on the arable site resulted in a significant reduction in hatching success among the birds nesting in the preferred habitat i.e spring cereal fields.

Sample sizes of hayfield clutches were too small to be so subdivided for inclusion in this part of the analysis.

Table 5.5. Nest survival in the two main study areas. p is the daily survival probability, v^2 its variance, and t was calculated from $p_1 - p_2 / \sqrt{v_1^2 + v_2^2}$ (Hensler and Nicholls 1981). Hatch success is the percentage of nests which hatched at least one egg ($p^{32} \times 100$).

YEAR	STUDY AREA	NESTS	NEST DAYS	CLUTCHES LOST	p	v^2	% HATCH SUCCESS	
1984	R.GRAZING	68	1165	28	0.976	2.0×10^{-5}	45.9	
								t=1.47,ns
"	ARABLE	75	1252	42	0.966	2.6×10^{-5}	33.5	
1985	R.GRAZING	54	747	31	0.958	5.4×10^{-5}	25.8	
								t=1.09,ns
"	ARABLE	27	348	20	0.942	1.6×10^{-4}	15.0	
1986	R.GRAZING	30	400	17	0.957	1.0×10^{-4}	24.9	
								t=0.28,ns
"	ARABLE	33	412	16	0.961	9.1×10^{-5}	28.1	
ALL	R.GRAZING	152	2312	76	0.967	1.4×10^{-5}	34.3	
								t=1.04,ns
	ARABLE	135	2012	78	0.961	1.9×10^{-5}	28.2	

Table 5.6. Nest survival in the two arable nesting habitats (spring cereals and hay). All three years combined. v^2 and t calculated by method of Hensler and Nicholls (1981). Hatch success is the percentage of nests which hatched at least one egg (p^{32} x 100).

HABITAT	NESTS	NEST DAYS	CLUTCHES LOST	p	v^2	% HATCH SUCCESS	
S.CEREALS	114	1640	71	0.956	$2.6X10^{-5}$	24.2	t=3.18,p<0.01
HAY	20	362	6	0.983	$4.6X10^{-5}$	58.5	

Table 5.7. Effect of timing of laying on nest survival among spring cereal and rough grazing clutches. Clutches separated into two time periods by first egg dates, before and on (a), or after (b) 15th April. All three years combined and v^2 and t calculated by method of Hensler and Nicholls (1981). Hatch success is the percentage of nests which hatched at least one egg (p^{32} x 100).

HABITAT		NESTS	NEST DAYS	CLUTCHES LOST	p	v^2	% HATCH SUCCESS
S.CEREALS	(a)	66	755	54	0.928	$8.8X10^{-5}$	9.3
	(b)	49	885	17	0.980	$2.2X10^{-5}$	53.7
R.GRAZING	(a)	83	1221	39	0.968	$2.5X10^{-5}$	35.3
	(b)	71	1121	37	0.967	$2.8X10^{-5}$	34.1

Predation

When losses due to cultivation are excluded (to avoid biassing the sample), there were no significant seasonal trends in predation intensity on either study area (Table 5.8). However, significantly fewer spring cereal than rough grazing clutches were predated (X^2 = 4.42, 1df, $p<0.05$, both time periods combined).

Table 5.8. Predation intensity in relation to season among spring cereal and arable clutches. Samples separated into two time periods according to first egg date, before and on (a), or after (b) 15th April. All three years combined and losses due to cultivation excluded (see text).

HABITAT		n NESTS NOT PREDATED	n NESTS WHICH LOST 1 OR MORE EGGS (%)	
SPRING CEREALS	(a)	23	21 (47.7)	$X^2 = 0.460$, ns
	(b)	29	20 (40.8)	
ROUGH GRAZING	(a)	38	45 (54.2)	$X^2 = 0.960$, ns
	(b)	27	44 (61.9)	

Despite the high levels of predation in both study areas, the predators responsible were identified in only seven cases: two clutches were thought to have been destroyed by avian predators (each of the eggs had been moved some distance from the nest and the contents removed through a single large hole which had been pecked in the shell). Five were likely to have been due to mammalian predators (eggs smashed and eaten in the nest). The commonest potential avian predators were crows and gulls, while the mammalian predators were most likely to have been either stoats, foxes or domestic dogs. In the remaining 113 predated clutches there were no clues to the identity of the predators. It is unlikely, however, that egg collecting by humans was an important factor, since in the many hundreds of hours spent in the study areas I came across suspected egg collectors only once. Most predation was due, therefore, to "natural" predators.

Breeding density

In 1984 and 1985 the nearest neighbour distances between nests on the rough grazing site were paced out (each pace was approximately 1m). The total sample was then subdivided into four distance categories and nest survival compared (Table 5.9). There were no significant

differences in daily survival probability between any combinations of distance categories (t <0.78). To avoid damaging the growing crops, this operation was not repeated on the arable site.

Table 5.9. Nest survival relative to nearest neighbour distance on the rough grazing study area in 1984 and 1985. p is the daily survival probability and hatch success is the percentage of nests which hatched at least one egg (p^{32} x 100).

	NEAREST NEIGHBOUR DISTANCE (m).			
	<26	26-50	51-100	>100
n OF NESTS	18	47	32	22
NEST DAYS	265	797	555	340
p	0.970	0.974	0.973	0.965
% HATCH SUCCESS	37.7	43.0	41.6	31.9

An alternative approach was then made by comparing the number of neighbouring rough grazing nests within a 100m radius of each nest which either hatched one or more eggs or which was entirely predated (Fig. 5.2). Although there was a tendency for a higher proportion of nests which were predated to have no neighbours within a 100m radius, the difference is not significant (X^2 test comparing the numbers of successful and unsuccessful nests which had none, with those that had one or more neighbours within 100m radius: $X^2 = 2.5$, $p>0.1$, 1 df). There is, therefore, no convincing evidence for a density dependent effect on hatching success over the range of densities encountered on the rough grazing site.

5.3.2 Fledging success and productivity

Factors influencing fledging success: egg size and hatchling body condition are intrinsic factors which have already been shown to influence chick survival (4.3.5). In this section putative extrinsic factors are considered:

a) Habitat: over the three years of the study taken together, fledging success was significantly poorer on the arable site than on the rough grazing site (Table 5.10; $X^2_{\text{all years}} = 6.06$, 1df, $p<0.05$). However, the difference was most marked in 1984 ($X^2 = 11.3$, 1df, $p<0.001$), less so in 1985 ($X^2 = 1.43$, 1df, $p<0.20$), and fledging success was similar on both sites in 1986.

Table 5.10. Fates of chicks on both study sites during the three years of the study. () = % fledging success. "Arable" = all arable crops combined.

HABITAT	YEAR	CHICKS DIED	CHICKS FLEDGED
ARABLE	1984	94	7(6.9)
	1985	35	6(14.6)
	1986	33	15(31.2)
	ALL	162	28(14.7)
ROUGH GRAZING	1984	95	27(22.1)
	1985	64	20(23.8)
	1986	36	16(30.8)
	ALL	195	63(24.4)

During the first two years of the study the arable chicks left their natal cereal fields shortly after hatching and moved to short pasture (Chapter 6). In those two years chick survival was poor and was influenced by the proximity of permanent pasture to the nest field. Chicks which hatched in spring cereal fields from which there was direct access to pasture had a higher fledging success. Chicks which had to cross intervening hay or cereal fields, or which had the River Forth to cross had a markedly lower success (Table 5.11). In 1986 crop growth was retarded by adverse weather and chicks stayed in their natal spring cereal fields. Fledging success, in that year, was

comparable to that on the rough grazing site (Table 5.10). The importance of brood movements in chick survival is considered in detail in the next chapter.

Table 5.11. The fates of arable chicks in 1984 and 1985 according to whether or not they hatched in cereal fields from which there was direct access to permanent pasture.

	n CHICKS DIED (%)	n CHICKS FLEDGED (%)
DIRECT ACCESS	22 (78.6)	6 (21.4)
		$X^2 = 3.34$, 1df, $p<0.07$
NO DIRECT ACCESS	74 (91.3)	7 (8.7)

b) Laying date: the possible influence of laying date on chick survival was investigated by separating rough grazing chicks into four categories according to the first egg dates of the clutches from which they hatched and comparing their fates (Table 5.12). Arable chicks were excluded from this part of the analysis because of the strong habitat influence on their survival pattern.

Table 5.12. Fates of rough grazing chicks according to the first egg dates of the clutches from which they hatched. All three years combined. X^2 value calculated by assuming that the proportions of chicks dying or fledging were unaffected by laying date.

	FIRST EGG DATE (DAYS AFTER 1st MARCH)			
	<46	47 - 61	62 - 76	>76
CHICKS FLEDGED (%)	37(26.6)	15(31.9)	11(25.0)	0(0.0)
CHICKS DIED (%)	102(73.4)	32(68.1)	33(75.0)	21(100)
		$X^2 = 8.42$, 3 df, $p<0.05$		

Chick survival was significantly affected by laying date. Survival among the the earliest three cohorts was similar but was lower in chicks from eggs laid late in the season. In addition to having a poorer survival, the late-hatched chicks grew more slowly (irrespective of their weight and size at hatching) than the earlier

chicks (6.3.3). This suggests that the higher mortality among the late-hatched chicks could be due to a deterioration in feeding conditions.

c) Weather: the first few days after hatching is the most vulnerable period of a chick's life (see below). The possible effects of weather on survival during this period were investigated by calculating the chill factor during the five days after hatching and comparing percentage survival among broods. The chill factor was given by: (20 - T) + R, where T is the mean 0900 hrs (GMT) temperature, and R the mean daily rainfall during the period (after Makepeace and Patterson 1980, Thompson et al. 1986). Because of the strong anthropogenic influence on their survival, arable chicks were excluded from this part of the analysis.

A regression of the Arc-Sine transformations of the percentages of broods which survived the five days after hatching against the chill factors during that period failed to reveal any significant trends ($n = 25$, $r = 0.05$). This result must, however, be treated with caution since it was often difficult to fix the exact date of chick death. Furthermore, chick survival may depend more on micro-climatic features e.g the amount of shelter afforded by the surrounding vegetation, than the gross measurements used in the calculation of the chill factors.

Timing of chick mortality

The mortality patterns of chicks in relation to their age were investigated in 1984 and 1985. In 1986, broods were not checked at frequent enough intervals to allow an accurate estimate of age at death.

The temporal mortality pattern was similar on both study sites in that most chick deaths occurred during the first 10 days after

hatching (Fig. 5.3). This post-hatching mortality was, however, much more severe on the arable site, where approximately 80% of chicks died before reaching 10 days old. The corresponding figure on the rough grazing site was about 50%. On the arable site the mortality rate was greatest during the first 5 - 6 days after hatching (the period during which they were transferring from spring cereals to pasture (Chapter 6)), but levelled out after 10 days. On the rough grazing site the initial mortality rate was less severe but did not begin to level out until about 16 days after hatching.

Productivity

During the first two years of the study, productivity was higher on the rough grazing than the arable study area (Table 5.13). The difference was most marked in 1984 (Mann-Whitney test: $z = -2.61$, $p<0.01$), and less so in 1985 ($z = -1.18$, $p<0.10$). In 1986 there was no significant difference in productivity between the two sites ($z = -0.34$, $p>0.30$). Females on the arable site laid a similar number of eggs but hatched fewer chicks than on the rough grazing site, though the difference was not significant ($z = -1.33$, $p<0.10$).

The mean numbers of attempts and eggs laid/female given in Table 5.13 for the arable study area are likely to be underestimates, since partially complete clutches on the spring cereal fields could have been destroyed by cultivation prior to detection.

Table 5.13. Reproductive effort and productivity of female Lapwings on the rough grazing and arable study areas. () = number of females.

		MEAN NUMBER OF:			
		ATTEMPTS/ FEMALE	EGGS/ FEMALE	HATCHLINGS/ FEMALE	FLEDGLINGS/ FEMALE
ROUGH GRAZING	1984 (30)	1.43	4.8	2.7	0.9
	1985 (25)	1.52	5.6	2.6	0.8
	1986 (19)	1.52	5.4	2.2	0.7
	ALL YEARS (74)	1.48	5.2	2.5	0.8
ARABLE	1984 (24)	1.37	4.7	2.0	0.2
	1985 (16)	1.62	6.0	2.1	0.4
	1986 (22)	1.60	5.4	2.2	0.7
	ALL YEARS (62)	1.52	5.3	2.1	0.4

5.4 DISCUSSION

Hatching success, fledging success and productivity differed greatly within and between the two study sites due to differences in the intensity of predation, pattern of land use, crop growth and timing of laying.

Hatching success and density dependent effects

Predation was the most important cause of failure to hatch on both study sites, accounting for approximately 75% of all egg losses. Egg predation was, however, more intense on the rough grazing site where, because of the hiding places offered by the numerous copses, isolated trees, rank areas of vegetation and dry stone walls, predators may have been commoner. Stoats and Foxes were seen far more frequently on the rough grazing site and Carrion Crows were certainly commoner (as evidenced by the numerous old and extant nests).

Hatching success on the arable site was reduced still further by egg losses during cultivation. Since most birds nested in spring

cereal fields and the start of laying coincided with that of cultivation, these losses were heavy. Lapwings are able to relay within a few days of losing a clutch and have the potential to make good these early losses. This, however, did not occur. Females on the arable site did not lay more eggs, and hatched fewer young than females on the rough grazing site. This could be explained either by females laying smaller replacement clutches, failing to relay altogether, or leaving the area and nesting elsewhere. It has already been shown (Chapter 4) that clutch sizes on the arable site during the early part of the season were smaller. This was probably due to the disruption to laying caused by cultivation. Moreover, all of the colour marked females which lost clutches during cultivation promptly relaid within a few hundred metres of their original nest site. In spite of extensive searches, no colour marked adult was ever found breeding outwith the study area (this, however, does not exclude the possibility of more distant movements). Thus, although it cannot be proven, it is likely that egg losses during cultivation helped reduce the final productivity of Lapwings on the arable site, since this led to birds ending up with smaller clutches than the normal four eggs. If a female is laying a clutch of four eggs (which takes a total of six or seven days) and her nest is destroyed by cultivation when the clutch is incomplete she may lay the remaining eggs in a new scrape and incubate only this partial clutch (Klomp 1951).

Breeding groups of Lapwings communally mob potential nest predators such as crows (Cramp and Simmons 1983). Since denser groups of Lapwings should be able to mount a more effective defence against such predators, they might be expected to show an enhanced hatching success. This, however, was not the case, i.e there was no density dependent influence on hatching success. Similar results were obtained by Elliot (1982), who studied hatching success among Lapwings in

different sized nesting groups. It is possible that the predator deterrence benefits obtained by nesting in denser or larger groups are counter-balanced by their increased conspicuousness and attractiveness to predators.

By concentrating their attentions on areas which supported a high density of broods, predators might have a density dependent effect on fledging success. However, since broods are highly mobile and change their position regularly, any estimate of "brood density" at the time of predation (which again cannot be obtained with any accuracy) would be suspect. For this reason it was not possible to investigate possible density dependent effects on chick survival. However, since distances between broods, even in the most densely populated areas, were normally in excess of 100 metres, such effects are, perhaps, unlikely.

Fledging success and productivity

The period of most severe chick mortality occurred on both study areas during the first few days after hatching. This early mortality is, apparently, widespread among the young of precocial species and is probably due, at least partly, to the initially poor efficiency of young chicks in regulating their body temperature and feeding. Cold, wet weather during the first few days after hatching might be expected to reduce chick survival through its effect on the availability of insect prey and by causing the chicks to stop feeding and seek more frequent brooding. The failure of this study to demonstrate such an effect may well be due to the relative crudeness of the methods used rather than its non-existence.

On the arable site the early mortality was more severe but of shorter duration than on the rough grazing site. This suggests that additional, habitat specific, mortality factors might be operating.

Both hatching and fledging success on the arable site were affected by the rate of crop growth and the prevailing land-use policy. During the first two years of the study the adults and broods were forced by crop growth to leave the natal spring cereal fields soon after hatching and move to pasture, the only short-grass habitat available (Chapter 6). A high chick mortality occurred during this movement between habitats, associated with a loss of weight and deterioration of body condition among those chicks which failed to reach suitable pasture early (Chapter 6). Chicks with direct access to suitable pasture undertook shorter or less hazardous journeys and survived better than chicks which hatched without easy access to pasture. This anthropogenic influence explains the initially more severe mortality on the arable site.

In 1986 crop growth was delayed by severe weather early in the spring, chicks were able to remain in their natal cereal fields after hatching and survived better than in the two previous years. Thus the habitat mix (in particular the accessibility of short grass pasture) and the timing of agricultural operations and crop growth in relation to that of breeding, was a major determinant of breeding success on the arable land.

As already noted (Chapter 3), adults preferred to nest in spring cereal fields which were close to pasture fields. Although, ultimately, this resulted in an enhanced chick survival and fledging success, the proximate mechanism behind this habitat choice need not necessarily involve the anticipation of the chicks needs. An alternative explanation is that the adults simply prefer to nest close to the pasture fields in which they feed.

The factors responsible for the earlier levelling out of the initial chick mortality on the arable site are not known but are likely to involve a lower intensity of predation. Once the initial

mortality has taken place there may be relatively few further losses due to the scarcity of predators. On the rough grazing site, however, predators are commoner and chicks may be exposed to a predation risk until later in development, when they may become more able to evade either detection or capture.

On the rough grazing site fledging success was low among later hatched chicks. This was associated with slower growth and poorer body condition (Chapter 6), and may have been caused by a reduction in food availability. Earthworms are known to burrow deeper during the summer months (Edwards and Lofty 1972), and leatherjackets metamorphose into adults. These organisms comprise an important food source for Lapwing chicks (Chapter 6), and their decreasing availability may explain the reduced chick survival. Thus, seasonal patterns of prey abundance might, ultimately, be an important influence on the timing of breeding in Lapwings. Further intensive work on the seasonal abundance patterns of the main prey species are required before such a relationship can be established.

Ring recovery studies suggest that the annual adult mortality of Lapwings is approximately 33% and the first year mortality is 44% (Bak and Ettrup 1982). However, ring recoveries consistently overestimate the mortality of waders (Evans and Pienkowski 1984). If, as seems likely, the true adult and first year mortalities of Lapwings are of the order of 25 -30 and 35 - 40%, respectively, then, assuming an equal sex ratio of chicks, each female in a hypothetical population would have to fledge on average 0.8 young/year if the population was to remain stable. This calculation assumes that emigration and immigration either do not occur or balance each other out.

Whereas the rough grazing females produced approximately enough fledglings to maintain their population in all three years of the study, the arable females only did so in 1986. Overall productivity on

the arable site was inadequate. Similarly low productivities were obtained during studies of Lapwings breeding on European arable land by Matter (1982) in Switzerland, Beser and Helden-Sarnowski (1982), and Kooiker (1984) in Germany.

The results of this and the three European studies referred to above raise the obvious question: why do Lapwings nest in a habitat (arable farmland) in which their breeding success is so low? It has already been demonstrated (Chapters 3 and 4) that feeding conditions for the adults are better on the arable site, resulting in better body condition, larger eggs and bigger and heavier chicks. However, given the reduction in productivity due to the land use policy, these benefits are only short-term and are unlikely to explain entirely the prevalence of arable nesting. It is more likely that certain changes which have occurred in the management of arable farmland over the last decade or two have resulted in it becoming a less suitable nesting habitat than it once was. This possibility is discussed further in Chapter 8.

Figure 5.1.

Clutch survival in relation to the stage of incubation. Sample sizes = 137 and 75 clutches at 0 and 27 days, respectively.

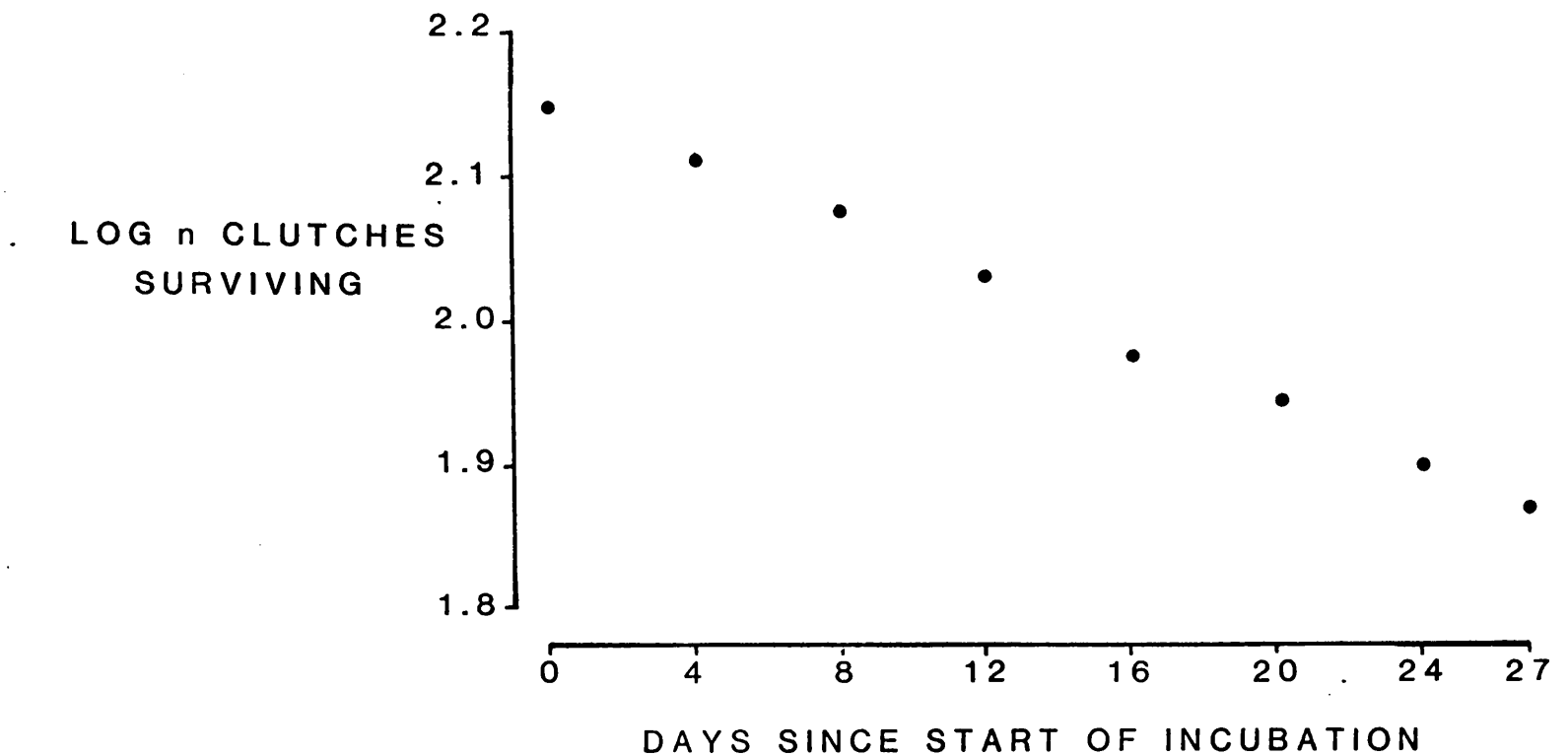

2.2
2.1
2.0
1.9
1.8
LOG n CLUTCHES SURVIVING
0
4
8
12
16
20
24
27
DAYS SINCE START OF INCUBATION

Figure 5.2.

Percent frequencies of nest densities on the rough grazing site. Upper = nests which hatched one or more eggs; lower = nests which failed entirely.

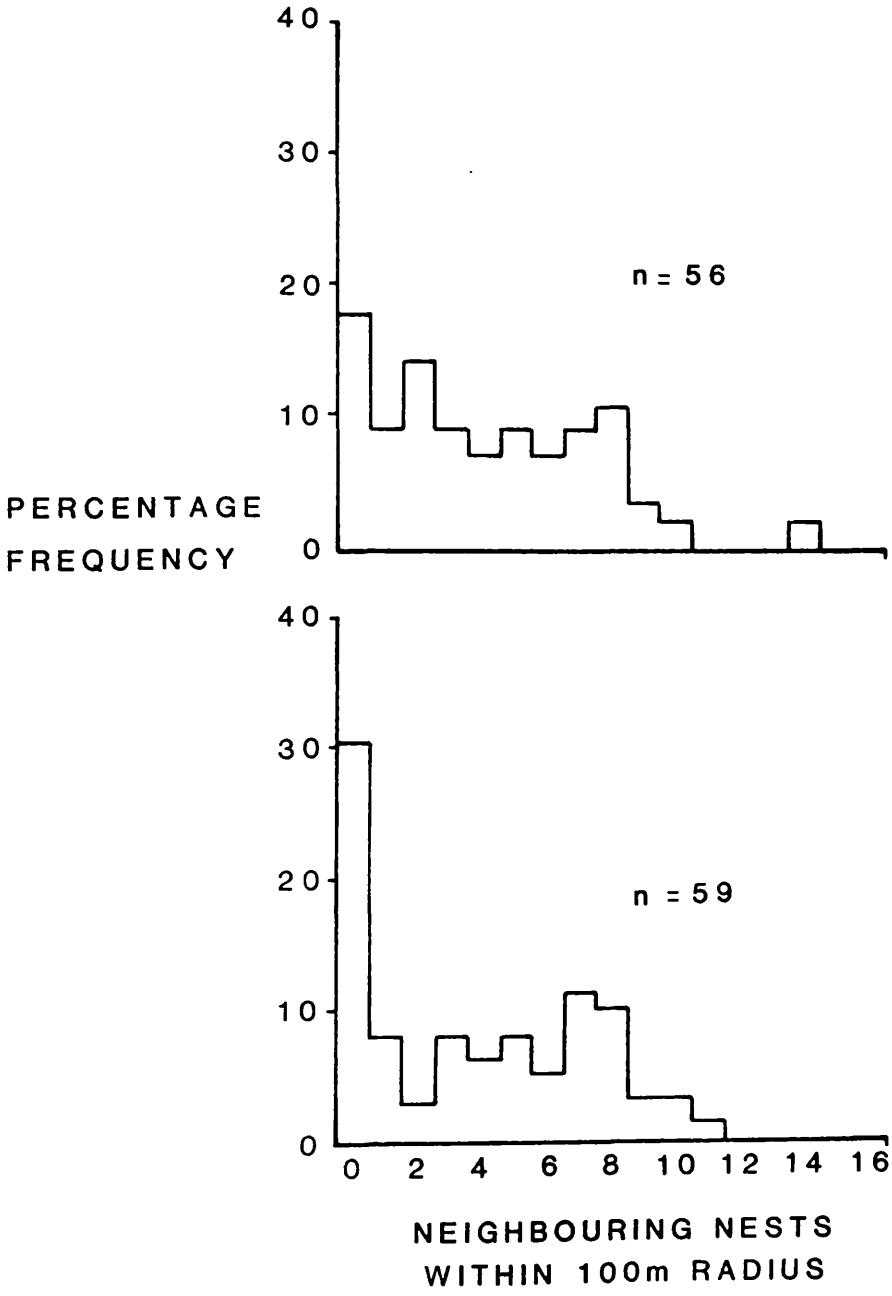
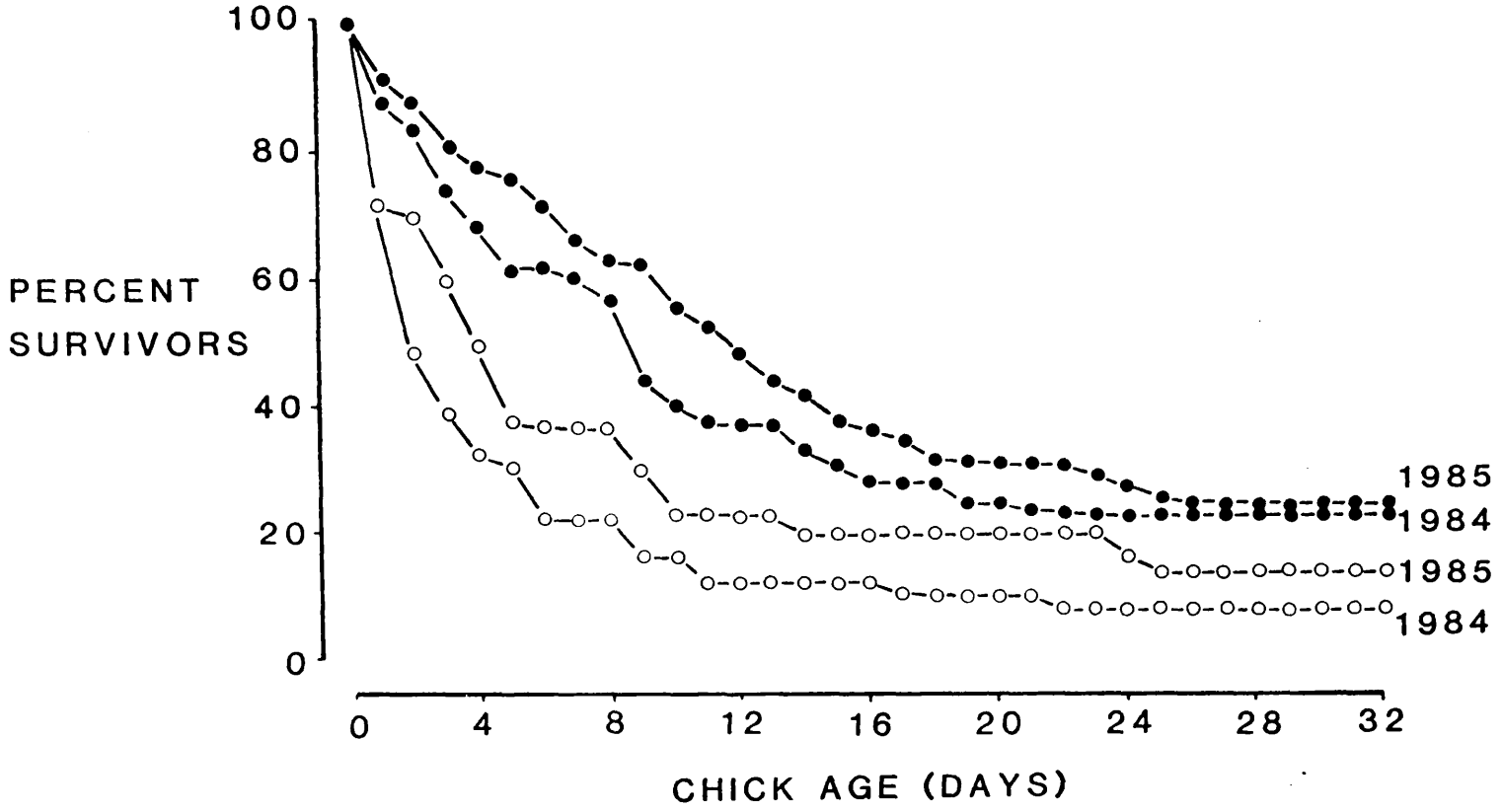

40
30
20
10
0
n = 56
PERCENTAGE
FREQUENCY
40
30
20
10
0
n = 59
0 2 4 6 8 10 12 14 16
NEIGHBOURING NESTS
WITHIN 100m RADIUS

Figure 5.3.

Chick survival curves on the rough grazing (closed symbols) and arable (open symbols) study areas. Initial sample sizes are: rougn grazing - 74 (1984), 59 (1985); arable - 49 (1984), 30 (1985).


100
80
60
40
20
0
PERCENT
SURVIVORS
0
4
8
12
16
20
24
28
32
CHICK AGE (DAYS)
1985
1984
1985
1984

Chapter 6 CHICK DIET, MOVEMENTS AND GROWTH

6.1 INTRODUCTION

Most wader chicks hatch into a hostile and demanding environment in which they must be able to feed themselves and evade their numerous predators largely by their own efforts. Consequently, acquiring the ability to find and secure food and avoid predators are likely to be major influences on their post-natal development (Lack 1968, O'Connor 1984), and we might expect to find growth and behavioural adaptations which are consistent with these ends.

An aspect of behaviour in which we might find such adaptations is in the selection and utilisation of suitable chick-rearing habitats. These areas must provide an adequate food supply and confer protection from predators. The importance of finding such sites is evidenced by the fact that wader families commonly undertake extensive and dangerous post-hatching movements to reach them (Hale 1980). There may, however, be constraints imposed by the chick's own morphology on the selection of chick-rearing habitat. For example, leg length may place limitations on the vegetation heights suitable for waders (Klomp 1951). Thus, habitat selection during the chick-rearing stage is likely to be the result of a compromise between the requirements for feeding and avoidance of predators, and the chick's own morphological limitations.

Chick growth involves an overall increase in body mass, together with changes in the relative proportions of the body components. Such allometric changes are generally thought to be the result of internal physiological constraints and selective pressures from the environment (Ricklefs 1979). This view of avian post-natal development assumes that resources for growth are in short supply and allocated in accordance with the current functional priorities of the neonate. For

example, nest-bound altricial chicks may undergo an initially rapid development of the feeding "organs" (i.e head and bill and gut), but are retarded in the development of their locomotory ability. Precocial chicks, which must be highly mobile, display a very different pattern.

Despite the interesting adaptations that are likely to be found in the growth patterns of precocial species, most studies have so far concentrated on altricial young. This is mainly due to the methodological problems inherent in working with precocial birds: since they are morphologically and behaviourally cryptic, and, since they may wander widely after hatching, they can be extremely difficult to locate and capture. The accumulation of adequate sample sizes can therefore be difficult. Altricial species, since they are confined to the nest or its immediate vicinity throughout their development, do not present these problems.

Since wader chicks may present these methodological difficulties to the extreme, it is not surprising that few satisfactory studies of their growth have been reported. This is so even for Lapwings, which are widely distributed, generally common, and which inhabit environments which are comparatively tractable. Thus, although at least three studies of the post-natal development of Lapwing chicks have been published (Jackson and Jackson 1975, Fuller 1983, Redfern 1983), they all suffer from small sample sizes, especially of known age chicks. Given these limitations, it has not been possible to draw conclusions, other than those which concern the general growth pattern of the species. The effects of environmental variables on growth rates and the adaptive significance of the mode of development have received little attention.

In spite of the methodological problems, adequate samples of chick measurements were obtained during this study. In this chapter, the growth, movements and habitat utilisation of lapwing chicks are

investigated in detail and the influence of food, predation and morphology assessed.

6.2 METHODS

6.2.1 Chick diet and movements

Chick diet was investigated using faecal analysis. Faeces collected (during normal ringing and measuring operations) from chicks feeding in a variety of habitats were stored in 70% alcohol for future analysis. The samples were subsequently teased apart in a petri dish and the fragments counted and identified to family level under a low power binocular microscope. Identification was aided by comparison with reference collections of invertebrates from both study sites.

The numbers of fragments of the most frequently encountered prey taxa were calibrated with the number of animals actually eaten by feeding whole invertebrates to a captive chick (collected under licence) and counting the fragments produced in the resulting faeces (Table 6.1).

The numbers of fragments found in the faeces of wild chicks were converted to the numbers of whole animals eaten by multiplying by the k values in Table 6.1 and dividing the result by the number of parts per animal. Body parts other than those listed in Table 6.1 (e.g elytra, wings, etc.) were found to be less useful for diet quantification since they were subject to extensive fragmentation during digestion. Less frequently found taxa were identified using a variety of other structures and the minimum numbers of whole animals eaten estimated by dividing the number of fragments by the number of component parts per animal.

Table 6.1. The component parts of 7 beetles, 4 beetle larvae, 4 spiders and 8 leatherjackets fed to a captive Lapwing chick and recovered in the resulting faeces. k = a conversion factor relating the numbers of fragments obtained to the numbers eaten, e.g $k_{beetle\ femora}$ = 42/35. The beetles included representatives of the Carabidae, Scarabaeidae, Staphylinidae and Curculionidae.

	NUMBER FED	NUMBER IN FAECES	k
BEETLE MANDIBLES	14	11	1.3
BEETLE FEMORA	42	35	1.2
BEETLE TIBIAE	42	38	1.1
BEETLE LARVAE - MANDIBLES	8	7	1.1
SPIDER FANGS	8	8	1.0
LEATHERJACKET MANDIBLES	16	13	1.2

In addition to the invertebrates listed in Table 6.1, six small to medium sized earthworms were fed to the captive chick. This resulted in a total of 2630 setae being recovered in the subsequent faeces, i.e 438 setae/earthworm eaten. This value was used to convert the numbers of setae found in the faeces of wild chicks to the actual numbers of earthworms eaten. However, because the time between ingestion and the voiding of the last setae was long (10 hours), because the number of segments and, therefore, setae per earthworm is highly variable (Edwards and Lofty 1972), and because the smaller, transparent setae can be very inconspicuous, the earthworm conversion factor is likely to be the least accurate of those used.

When the captive chick was being fed experimentally its faeces were collected as they were produced and analysed separately. This method showed that all taxa, excluding earthworms, were represented in the faeces within 60 minutes of ingestion and stopped appearing some four hours afterward.

The estimated frequencies of prey items in the diet were converted to approximate biomasses by drying 10 medium sized representatives of each of the taxa: Carabidae, Curculionidae, Staphylinidae, Beetle larvae, Tipulid larvae (Leatherjackets), Aranea and Lumbricidae to a constant weight. The mean dry weight of individuals was then calculated and the numbers eaten multiplied accordingly.

During regular checks on chick survival the locations of broods were plotted on 1:10000 maps and the habitats were recorded as either pasture, spring cereal, winter cereal or hay (arable site), improved or unimproved rough grazing.

6.2.2 Chick ageing

Almost half of the chicks from which biometrics were obtained had been ringed while still in the nest and were, therefore, of known age. Linear regressions were fitted to plots of the measurements of these chicks against days from hatching (y axis) and the resulting regression equations used to estimate the ages of chicks of unknown hatching dates. Throughout the linear phase of its growth, head and bill length gave the most accurate prediction of age: days from hatching = 1.05 x H&B length(mm) - 33.74 ($r = 0.97$; s.e = 1.42; $n = 353$; mean deviation from regression = 0.7 days). About 22 days after hatching head and bill length becomes a less accurate predictor of chick age since its growth slows, and some other parameter must be used. From 22 days onward the length of the 9th primary gave the most accurate estimate: days from hatching = 0.13 x 9th primary length(mm) + 21.28 ($r = 0.76$; s.e = 3.43; $n = 32$; mean deviation from regression = 2.4 days). Thus, by using these two measurements, chicks less than or older than 22 days could be aged with mean errors of less than a day, and 2.4 days respectively. Weights, wing, bill, tarsus and foot

lengths were found to be less accurate predictors of chick age.

6.3 RESULTS

6.3.1 Chick diet

The results of the analysis of 10 faeces from different chicks in each study area are shown in Table 6.2. In both study areas chicks fed on both soil and surface-living invertebrates. Soil invertebrates (Tipulid larvae, Lumbricidae) were eaten in only small numbers, but, because of their larger size, they comprised the greater part of the prey biomass. Chicks on the rough grazing site ate more surface-living prey and fewer soil invertebrates (36% and 64% of dry weight, respectively) than chicks on the arable site (25% and 75%). This habitat difference was due mainly to the arable chicks eating fewer Scarabaeid and Carabid beetles and spiders, but more Tipulid larvae than the rough grazing chicks. Invertebrate sampling (6.3.2) showed that whereas the numbers and biomasses of surface invertebrates were comparable in the chick feeding habitats of the two study areas, soil invertebrates were comparatively scarce in the rough grazing feeding areas. The difference in chick diet between the two study areas is, therefore, a reflection of differences in the invertebrate communities. Regressions of Arc-Sin transformations of the percentage frequency of the various prey taxa in each faecal sample against the age of the chicks which produced the sample failed to reveal any significant dietary trend with age.

In addition to the items listed in Table 6.2, many faeces contained small quantities of plant material which may have been inadvertently ingested with the animal prey.

Table 6.2. Estimated frequencies and dry weights (mg) of invertebrates in the diet of Lapwing chicks in the two study study areas. "Others" are mainly Formicidae and adult dipterans.

TAXON	n OF INDIVIDUALS	% OF TOTAL n	INDIVIDUAL MEAN d.w.	TAXON d.w.	% OF TOTAL d.w
ARABLE:					
SCARABAEIDAE	35	20.8	0.9	31.5	6.1
CARABIDAE	10	5.9	1.4	14.0	2.7
CURCULIONIDAE	16	9.5	0.9	14.4	2.7
STAPHYLINIDAE	5	2.9	0.7	3.5	0.7
CHRYSOMELIDAE	4	2.3	0.5	2.0	0.4
BEETLE LARVAE	9	5.3	1.1	9.8	1.9
TIPULID LARVAE	32	19.0	3.6	115.2	22.4
ARANEA	16	9.5	1.1	17.6	3.4
LUMBRICIDAE	8	4.8	34.2	273.6	53.1
OTHERS	33	19.6	1.0	33.0	6.4
TOTALS	168			514.6	
ROUGH GRAZING:					
SCARABAEIDAE	96	42.4	0.9	86.4	15.5
CARABIDAE	25	11.1	1.4	35.0	6.2
CURCULIONIDAE	13	5.7	0.9	11.7	2.1
HISTERIDAE	6	2.6	0.9	5.4	0.9
HYDROPHILIDAE	5	2.2	0.9	4.5	0.8
STAPHYLINIDAE	6	2.6	0.7	4.2	0.7
CHRYSOMELIDAE	1	0.4	0.5	0.5	<0.1
BEETLE LARVAE	6	2.6	1.1	6.5	1.1
TIPULID LARVAE	14	6.2	3.6	50.4	9.0
ARANEA	24	10.6	1.1	26.4	4.7
LUMBRICIDAE	9	3.9	34.2	307.8	55.2
OTHERS	18	8.9	1.0	18.0	3.2
TOTALS	223			556.8	

6.3.2 Brood movements and food availability

70% of Lapwing nests on the arable site were on spring cereals and over 90% on the rough grazing site were on unimproved rough grazing. However, during the first two years of the study (and in the final year on the rough grazing site) the chicks left these habitats shortly after hatching to move to pasture fields (the arable site) or improved rough grazing, ditches and damp flushes (Figures 6.1 - 6.2). Unless disturbed, they remained in these habitats until fledging. The distances travelled during these movements depended on the position of the nest relative to suitable chick-rearing habitat, but were normally between 100 and 400 metres (straight-line distance). The longest recorded movement during this study was 1500 metres, but this was a brood of chicks which were close to fledging and which I had disturbed from their normal area by catching and measuring them.

Not all pasture fields were equally attractive to broods on the arable site. Fields which were only lightly grazed and in which the grass was long were avoided, while heavily grazed fields of short grass seemed to be preferred. These apparent preferences were tested in 1985 by regularly censussing the broods in all 18 of the pasture fields on the arable site and converting the maximum count to maximum brood density (MBD) by dividing by field area. A measure of the grass height in each field was obtained by randomly throwing a 1/4 m^2 quadrat 10 times in each field, measuring the grass height at each corner and using the results to calculate the mean grass height (MGH). The grazing intensity was assessed by counting the number of cowpats within a circular quadrat 5m in radius from the center of each randomly thrown quadrat and calculating the mean cowpat density (MCD). Since stock was regularly moved between fields to optimise grazing potential, MCD is thought to be a better indicator of grazing intensity than simple counts of grazing animals. MCD was negatively

correlated with MGH ($r = -0.58$, $p<0.02$) indicating that intensive grazing results in a shorter sward. The factors contributing to the "attractiveness" of particular pasture fields were investigated using a stepwise multiple regression analysis in which MBD was the dependent variable and field area, MCD and MGH were the independent variables. Only MGH contributed significantly to the variation in MBD between fields (42.2% of the variation explained - Figure 6.3), giving a regression equation of: MBD = -5.13MGH + 56.7. Thus, chicks on the arable site moved to pasture fields soon after hatching and preferred those in which the grass was kept short by intensive grazing.

To determine whether these brood habitat changes were related to potential prey distribution, the invertebrate densities and biomasses in the two main nesting habitats (spring cereals, unimproved rough grazing) were compared with those in the two main chick-rearing habitats (short pasture, improved rough grazing) by a combination of soil sampling and pitfall trapping. The nesting habitat samples were collected in areas in which Lapwings nested but which were later deserted by the broods, while the samples from the chick-rearing habitats were collected from areas regularly frequented by these same broods. Surface-living invertebrates were sampled in each habitat in late May and early June (the main chick-rearing period) by placing pitfall traps in a transect line at intervals of ten metres for periods of between 7 and 10 days. The use of pitfall traps to compare invertebrate populations in markedly different habitats has been criticised (Mitchell 1963). However, it was felt that within each of the two study areas the nesting and chick-rearing habitats were sufficiently alike to minimise any potential bias. To avoid excessive disturbance during nesting, the soil samples were collected in February and March. Although the available biomass of soil invertebrates may have altered between sampling and chick-rearing due

to growth, mortality, pupation, aestivation and deeper burrowing by earthworms (Boyd 1958, Coulson 1962, Dunnet 1955, Edwards and Lofty 1972), it is felt that the relative differences between nesting and chick-rearing habitats were so great as to be unlikely to be substantially altered.

The numbers and biomasses of sub-surface potential prey, which represent 75% and 64% of the dry mass of consumed prey of Lapwing chicks in arable and rough grazing, respectively, were higher in the areas to which broods moved after hatching than in the nesting areas themselves (Tables 6.3). On the rough grazing site surface invertebrates were also more abundant in the chick-rearing areas. This, however, was not the case on the arable site (Table 6.4).

Table 6.3. Mean numbers and dry weights (mg) of soil invertebrates in $1/25m^2$ and 10cm deep soil samples from nesting (spring cereals, unimproved rough grazing) and chick-rearing habitats. Asterisks indicate significance levels when Mann-Whitney tests were carried out: * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.

		LUMBRICIDAE		TIPULID LARVAE	
HABITAT	n OF SAMPLES	MEAN n/ SAMPLE	MEAN d.w/ SAMPLE	MEAN n/ SAMPLE	MEAN d.w/ SAMPLE
ARABLE:					
SPRING CEREALS	15	5.1 ***	128 ***	0.8 ***	5 ***
PASTURE	15	20.3	881	15.5	182
ROUGH GRAZING:					
UNIMPROVED	18	0.9 **	18 ***	1.3 **	11 **
IMPROVED	20	2.3	102	4.0	32

Table 6.4. Mean numbers and dry weights (mg) of surface invertebrates caught in pitfall traps on nesting (spring cereals, unimproved rough grazing) and chick-rearing habitats. Asterisks indicate significance levels when Mann-Whitney tests were carried out: * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.

HABITAT	n TRAP/DAYS	MEAN NUMBERS/ TRAP-DAY	MEAN DRY WEIGHT/ TRAP-DAY
ARABLE:			
SPRING CEREALS	143	0.2	4.9
PASTURE	123	0.4	2.1
ROUGH GRAZING:			
UNIMPROVED	250	1.8 ***	0.8 **
IMPROVED	115	4.0	1.4

In 1986 chick movements on the arable site deviated from the pattern established in the two previous years (Fig. 6.4). Due to cold, wet weather in the early spring, crop growth had been retarded. When the chicks hatched the height of the spring cereals was approximately half what it had been in the two preceeding years and this difference was maintained throughout the chick fledging period. Moreover, some areas of crops failed entirely due to water-logging, leaving patches of bare ground in the growing crop. In that year, many chicks remained in the vicinity of the nest site or patches of bare ground until close to fledging.

6.3.3. Chick growth

All of the chick measurements used in this section were obtained during 1984 or 1985.

The general pattern of growth

The general pattern of chick growth is shown in Figures 6.5 to 6.8, and chick growth relative to adult dimensions in Figure 6.9. The adult dimensions used in the construction of Figure 6.9 were obtained from

71 birds caught on the Clyde Estuary during the months July - September (1980 - 1981), and 27 breeding birds caught during the course of this study (Table 6.5).

Table 6.5. Adult dimensions used in the construction of Figure 6.9. Sources are birds caught during this study and on the Clyde Estuary during July - September (1980-1981). Lengths in mm and weight in gms.

PARAMETER	n OF BIRDS	MEAN	s.d.	SOURCE
WING LENGTH	60	232	6.02	BOTH
BILL LENGTH	26	23.6	1.52	THIS STUDY
FOOT LENGTH	27	80.6	2.55	" "
WEIGHT	98	228	8.01	BOTH

On hatching, Lapwing chicks have well developed legs (relative to mature dimensions), less well developed bills and poorly developed wings (Figure 6.9). Whereas the rate of leg growth is constant throughout the fledging period, bill growth is initially rapid, but becomes less so after 12 days from hatching. Wing growth, although slow at first, speeds up after about 8 days from hatching. Fledging normally occurs at about 35 days after hatching (Spencer 1953, pers obs.), and at this time the hatchling pattern of relative proportions persists, although the differences have been reduced. The average dimensions of 6 fledged chicks (i.e chicks which flew when released) are shown in Table 6.6.

Table 6.6. Average dimensions of 6 Lapwing chicks which were capable of flight when released. Lengths in mm and weight in gms.

PARAMETER	MEAN	s.d	% OF ADULT DIMENSIONS
HEAD AND BILL LENGTH	56.8	1.05	92.2
BILL LENGTH	21.7	1.01	83.4
FOOT LENGTH	75.2	1.47	93.3
WING LENGTH	170	7.06	73.2
WEIGHT	161	10.68	70.6

Factors affecting growth

Chick growth rates were compared using weights and head and bill lengths (head and bill length was the most precise of the body measurements), while the quotient (weignt/head and bill length) was used as an index of body condition.

a) Years. Because neither head and bill nor weight grew linearly (Figs 6.5 and 6.7), two phases of growth were considered: 0-20 and >20 days from hatching (head and bill), and 0-5 and >5 days from hatching (weight). T-tests and covariance analysis failed to reveal any significant between-year differences in chick growth rates in either study area (Tables 6.7, and 6.8) and for the remainder of the analysis data from both years are combined.

Table 6.7. Chick head and bill and weight growth rates compared between 1984 and 1985 (the years when most chick biometrics were obtained) using covariance analysis.

PARAMETER	CHICK AGE(days)	ROUGH GRAZING F_{slopes}	d.f	p	ARABLE F_{slopes}	d.f	p
HEAD AND BILL LENGTH	0-20	0.08	2/380	ns	0.62	3/278	ns
" " " "	>20	0.20	2/63	ns	0.28	3/46	ns
WEIGHT	>5	0.00	3/231	ns	2.48	3/163	ns

Table 6.8. Chick weights in 1984/85 (the years when most chick biometrics were obtained) compared using T-tests.

CHICK AGE (DAYS)	ROUGH GRAZING MEAN WEIGHTS(g) 1984/85	t	d.f	p	ARABLE MEAN WEIGHTS(g) 1984/85	t	d.f	p
0 - 1	17.9/17.7	0.71	131	ns	17.8/18.1	0.86	235	ns
2 - 3	18.7/18.7	0.05	54	ns	18.7/17.6	1.13	93	ns
4 - 5	22.1/21.8	0.14	27	ns	21.1/20.3	0.56	19	ns

b) Habitat. When chick habitats were categorised as either rough grazing or arable no differences in growth were detected (Figs 6.10 and 6.11). Significant differences did, however, become apparent when these habitat categories were further subdivided. During their post-hatching movements from their natal spring cereal fields to pasture fields arable Lapwing chicks lost weight (Fig. 6.12). This loss was made good when the chicks reached the pasture fields and by the time that they were 9-10 days old their weights were not significantly different from their contemporaries on rough grazing (Mann-Whitney test: $U = 78$; $n = 11/19$; ns). However, those arable chicks which failed to reach pasture fields continued to lose weight (Fig. 6.12), until, by the time they were 3-4 days old, they were significantly lighter than their contemporaries which had reached pasture (Mann-Whitney test: $U = 10$; $n = 16/5$; $p<0.02$), and were approximately 45% lighter by the age of 7-8 days. In spite of their continual weight loss, chicks remaining in cereal fields increased in size (although at a slightly slower rate than their contemporaries on rough grazing or pasture fields) at least up until they were 5-6 days old (Fig. 6.13). This structural growth combined with their decreasing weights resulted in a gradual deterioration in body condition among the chicks remaining in the cereal fields (Fig. 6.14), accompanied by a high mortality (Chapter 5).

On the rough grazing site the post-hatching movement between unimproved and improved habitat normally took only a few hours and early weight losses did not persist (Fig. 6.12).

c) Size and weight at hatching. Initial chick size (denoted by head and bill length) and weight affect subsequent size and weight up until 5-6 days after hatching. Initial body condition apparently affects subsequent body condition until at least 16-17 days after hatching (table 6.9).

Table 6.9. Correlation coefficients between chick size (head and bill length), weight and body condition (weight/head and bill length) at hatching and at subsequent recaptures. Arable chicks are not included in this table because of small sample sizes and habitat-dependent differences in growth patterns. * = $p<0.10$; ** = $p<0.05$; *** = $p<0.01$. () = number of chicks measured at hatching and recaptured subsequently.

	DAYS FROM HATCHING			
PARAMETER	3/4(11)	5/6(8)	13/14(12)	16/17(10)
WEIGHT	0.58*	0.74**	0.45	0.47
HEAD AND BILL LENGTH	0.59*	0.94***	0.09	-0.20
BODY CONDITION	0.50	0.59*	0.45	0.58**

d) Hatching date. Survival among late-hatched rough grazing chicks is poor in comparison to chicks hatched earlier in the season (Chapter 5). In this section the likelihood that these mortality differences are accompanied by growth differences is investigated. Arable chicks were excluded from this analysis because of the strong anthropogenic influence on their growth and survival.

The effects of hatching date on chick growth were investigated by separating the rough grazing chicks into three categories (hatched before 9th May; hatched between 9th May and 29th May, and hatched after 29th May), by allocating the chicks within these categories to six age classes and by carrying out T-tests between the means of each

(Fig. 6.15).

The differences between the age class means of middle and early and middle and late hatched chicks were not significant. However, late hatched chicks were significantly lighter than early hatched chicks at 4-7 days ($t = 2.80$, $p<0.001$), 8-11 days ($t = 3.59$, $p<0.001$) and 12-17 days ($t = 3.06$, $p<0.01$). There were no significant weight differences at hatching but there were between early and late hatched chicks when weights at ages 1-3 days were compared ($t = 3.12$, $p<0.01$), indicating that the weight discrepancy between the two cohorts becomes established soon after hatching. In addition to being significantly lighter in body weight, the heads and bills of late hatched chicks were significantly smaller than those of early hatched chicks at ages 0-3 days ($t = -4.57$, $p<0.001$), 7-11 days ($t = 2.17$, $p<0.05$) and 12-17 days ($t = 2.56$, $p<0.01$), and their body conditions poorer ($t = 4.79$, $p<0.001$; $t = 3.13$, $p<0.01$; $t = 3.57$, $p<0.01$; and $t = 1.73$, $p<0.10$, respectively). Neither head and bill nor body condition were significantly different at hatching (h&b: $t = -0.93$; b.c.: $t = 0.80$). These data indicate that although early and late broods hatch at comparable sizes and body conditions, a retardation in growth rate and a deterioration in body condition affect the late hatched chicks soon after.

By 17-23 days there were no significant differences in either weights, head and bill lengths or body condition between early and late hatched chicks (Fig. 6.15). This convergence is unlikely to be due to late hatched chicks accelerating growth: the mean growth rates of 20 chicks trapped and retrapped between the ages of 3 and 17 days were not significantly different from those of 7 chicks trapped and retrapped between 17 days old and fledging (3-17 = 3.4 g/day; >18 = 2.9 g/day; Mann-Whitney test: $U = 59.5$). A more likely explanation for the weight convergence is that the smaller and lighter late

hatched chicks suffer a higher and earlier mortality than their larger and heavier contemporaries. In this event the cohort would become increasingly composed of heavier and presumably fitter chicks. This would result in an apparent increase in growth rate when their weights are displayed as in Fig. 6.13. Unfortunately, data are too few to assess the validity of this hypothesis.

e) Weather. Possible weather effects on chick growth were sought among rough grazing chicks between 5 and 10 days old (by which age the weights of most chicks were increasing but they still relied on the parents for frequent brooding). A stepwise multiple regression analysis was carried out with chick weight as the dependent variable and age, hatching date and chill factor as the independent variables. Chill factors were calculated from: (20 - T) + R (after Makepeace and Patterson 1980, and Thompson et al. 1986), where T was the mean 0900 hrs (GMT) temperature, and R the mean daily rainfall over the five days preceeding weighing.

Whereas age and hatching date did contribute significantly to the total variation in chick weight, chill factor did not (Table 6.9). This suggests that inclement weather had little or no effect on chick growth (likewise survival - Chapter 5). However, this result should be treated with caution since chick feeding efficiency and growth might depend more on the micro-climatic features of their immediate environment (e.g the shelter afforded by the surrounding vegetation) than the gross measurements used in the calculation of chill factors.

Table 6.9. Results of a stepwise multiple regression of the weights of 42 rough grazing chicks between 5 and 10 days old with three independent variables.

PARAMETER	r	% OF VARIATION EXPLAINED	b	F	p
AGE	0.57	32.7	3.23	12.3	<0.01
HATCH DATE	-0.36	8.8	-0.19	5.8	<0.05
CHILL FACTOR	<0.01	-	-0.15	0.1	ns

6.4 DISCUSSION

Chick diet

Although the diets of adult waders on their winter and passage habitats has been well studied (refs in Evans et al. 1984), remarkably little has been published on chick diet. In populations of Calidridine sandpipers breeding on nearctic tundra, the diet of the chicks is dominated by the extremely abundant chironomid (Diptera) larvae (Holmes and Pitelka 1964). In temperate areas, however, where the invertebrate communities are more diverse and less affected by seasonal flushes of particular species, the few studies which have been published suggest that chick diet is more varied and less dependent on particular taxa. Yalden (1986), showed that the diet of Common Sandpiper Actitis hypoleucos chicks was characterised by a wide variety of invertebrate prey species, including both surface and soil organisms. Although Yalden (1986) did not convert his prey frequencies to biomasses, it is evident that earthworms, which numerically comprised only a small proportion of the prey taken, were an important component of the total biomass (especially when the chicks were feeding in improved pasture where, presumably, earthworms were more abundant). On agricultural land in Switzerland, Lapwing chicks exploited a wide prey spectrum but earthworms and dipteran larvae

(mainly Tipulidae) comprised between 15% and 28% of the total prey items (Matter 1982).

This study has shown that on Scottish agricultural land, the numerical composition of Lapwing chick diet is influenced by prey availability and habitat differences in the invertebrate communities. Thus, on the rough grazing feeding areas where soil invertebrates (earthworms and leatherjackets) were less abundant, the chicks ate more surface species (mainly beetles and their larvae). Although soil invertebrates comprised the major part of the prey biomass, they were taken in comparatively small numbers, which suggests that the chicks were feeding opportunistically rather than selectively.

Growth

The general pattern of development of Lapwing chicks is closely adapted to their ecological circumstances during the pre-fledging period. Apart from avoiding predation (for which the combination of cryptic behaviour and colouration is important), the main requirements facing the hatchling are that it must be capable of moving to a suitable , but possibly distant, feeding site, and be able to secure its own food. For these requirements to be met, the chick must hatch with an already well developed locomotory and food processing capability, together with efficient neuro-muscular coordination and sense organs (particularly eyes, since Lapwings are visual hunters).

On hatching, Lapwing chicks do have relatively large eyes; they are able to catch small, fast-moving prey such as Carabid and Staphylinid beetles, and their legs and head and bills are well developed relative to the rest of their body. Further rapid leg and head and bill growth takes place during the first half of the nestling period. Of the two components, the legs are most advanced at hatching but, by the age of 10 days, rapid head and bill growth has

substantially reduced the difference. This pattern of development would have adaptive significance if, as seems likely, the priority at hatching is to leave the nest site and reach a more or less distant chick-rearing area. During this early stage, the chicks may have little time for feeding, since they must follow their parents and are brooded frequently, and they may have to rely on their yolk reserves. The depletion of these reserves probably explains the initial weight reduction in the first day or two after hatching (Fig. 6.6). Rapid head and bill growth may become necessary, however, once the chick-rearing area is reached and serious feeding begins.

During the early stages of growth, when locomotion and feeding capability are successive priorities, the chick's wings remain poorly developed relative to the legs and head and bill. This remains so until about 10 days after hatching when an acceleration in wing growth begins. This rapid growth is then maintained throughout the rest of the pre-fledging period. The weight increase mirrors that of wing length, with little net change during the first week, followed by an exponential phase. This might indicate that wing growth, although ultimately crucial if predation is to be avoided, has a low priority at first, with resources only becoming available once the chick is feeding efficiently and its weight is increasing rapidly. Nevertheless, since flight capability is attained when the chick's weight is only 70% that of adult weight (Jackson and Jackson 1975, Fuller 1983, and Redfern 1983 obtained similar results), wing development must become a high priority once the rapid phase of weight increase has begun.

While the general growth pattern of Lapwing chicks may be adaptive and genetically pre-determined, additional intrinsic and environmental factors may also have an effect. At least three factors may be important: a) Size at hatching. Chapter 4 demonstrated that

chicks which hatch from large eggs are larger and heavier and survive better than chicks from small eggs. Subsequent size and growth is also influenced by hatchling size and weight, i.e chicks which hatch larger and heavier retain this advantage during at least the first two weeks of development. Thus egg size affects chick growth, as well as survival. Since egg size is partly determined by maternal body condition (which is influenced by food availability), habitat quality exercises an indirect effect on chick growth as well as their survival. b) Habitat heterogeneity. On the arable site, nesting field size and crop in the adjoining fields partly determined whether chicks had easy access to pasture (the chick-rearing habitat in two of the three years). Those which did not have easy access failed to reach pasture quickly, lost weight and suffered a higher mortality (Chapter 5) than those which had. Thus habitat heterogeneity and patch size, i.e the "grain" of the environment is important for both the growth and survival of Lapwing chicks. Current agricultural trends toward field amalgamation and monoculture cultivation could, therefore, have important implications for Lapwing population processes. This is discussed further in Chapter 8. c) Season. Chicks which hatched from eggs laid late in the year grew (and survived - Chapter 5) less well than earlier hatched chicks. This, as has already been discussed in Chapter 5, may be related to a probable seasonal deterioration in the food supply.

Brood movements and habitat utilisation

In all three study years on the rough grazing site and in two of the three on the arable site, hatching was immediately followed by a general movement of broods from the nest-site habitat (spring cereals, unimproved rough grazing) to what were to be the chick-rearing habitats (permanent pasture and improved rough grazing or ditches,

respectively).

Comparable habitat changes have been found during other Lapwing studies: Redfern (1982) found that chicks which hatched on a Scottish peat bog moved quickly to adjacent, more fertile pasture, and Matter (1982) reported that Lapwings nesting in a marsh in Switzerland led their newly hatched chicks to pasture or mown meadows.

On the arable site, the duration of the post-hatching movement was, apparently, a dangerous time for the chicks, since it coincided with a deterioration in body condition and a high mortality among those which did not reach pasture quickly (Chapter 5). Nesting in cereal fields and unimproved rough grazing is likely to be advantageous in that the eggs and incubating females are highly cryptic (Chapter 3). However, what advantage do the chicks gain by undertaking what may be a hazardous journey to improved rough grazing or pasture? The areas into which the chicks move are certainly richer in food but this is not, apparently, the only reason for the move, at least on the arable site. In 1986 the growth of the crops was retarded and patchy and the chicks remained in their natal cereal fields, until they were near fledging. This suggests that the crop height may be an important factor in determining whether or not the chicks undertake post-hatching movements. Lapwing chicks have comparatively short legs for a wader and walking is impeded by long dense vegetation (Klomp 1951). Furthermore, tall vegetation may interfere with the parents ability to watch over their chicks. In normal years crop growth quickly renders the spring cereal fields unsuitable as a chick rearing habitat and the broods must move to the only short-grass habitat available, heavily grazed permanent pasture.

On the rough grazing site the height of the vegetation in improved and unimproved rough grazing was little different during the chick-rearing period and the post-hatching movement may have been due

mainly to food availability.

Once in the chick-rearing habitat, the risk of predation may be important in determining where the chicks actually feed: on the arable site they stayed close to the edges of pasture fields and when disturbed they ran into the adjacent cereal fields where they could hide in the long vegetation. In the ditches or improved areas of the rough grazing site their distribution was apparently influenced by that of Juncus clumps and broken areas of ground. Chicks fed in the open on the short pasture or the muddy ditch margins but fled into cover when disturbed.

Thus, at least three factors influenced the post-hatching movements and habitat utilisation by Lapwing broods: food availability, the risk of predation, and the chick's own morphological limitations, i.e its ability to cope with the density and height of the surrounding vegetation.

In summary: although the growth pattern and behaviour of Lapwing chicks may be influenced by short-term environmental factors, they are, nevertheless, intimately adapted to the ecological requirements of the chick's life-style. They may be viewed as the result of a compromise between interacting and, perhaps, conflicting selective pressures (such as the need to be highly mobile, to avoid predators and be able to exploit prey organisms which may be difficult to capture), and the chick's own morphological constraints.

Figure 6.1

Habitat use by recently hatched broods of Lapwings on the arable study area during 1984 and 1985. Open and closed symbols refer to spring cereal and permanent pasture fields, respectively.

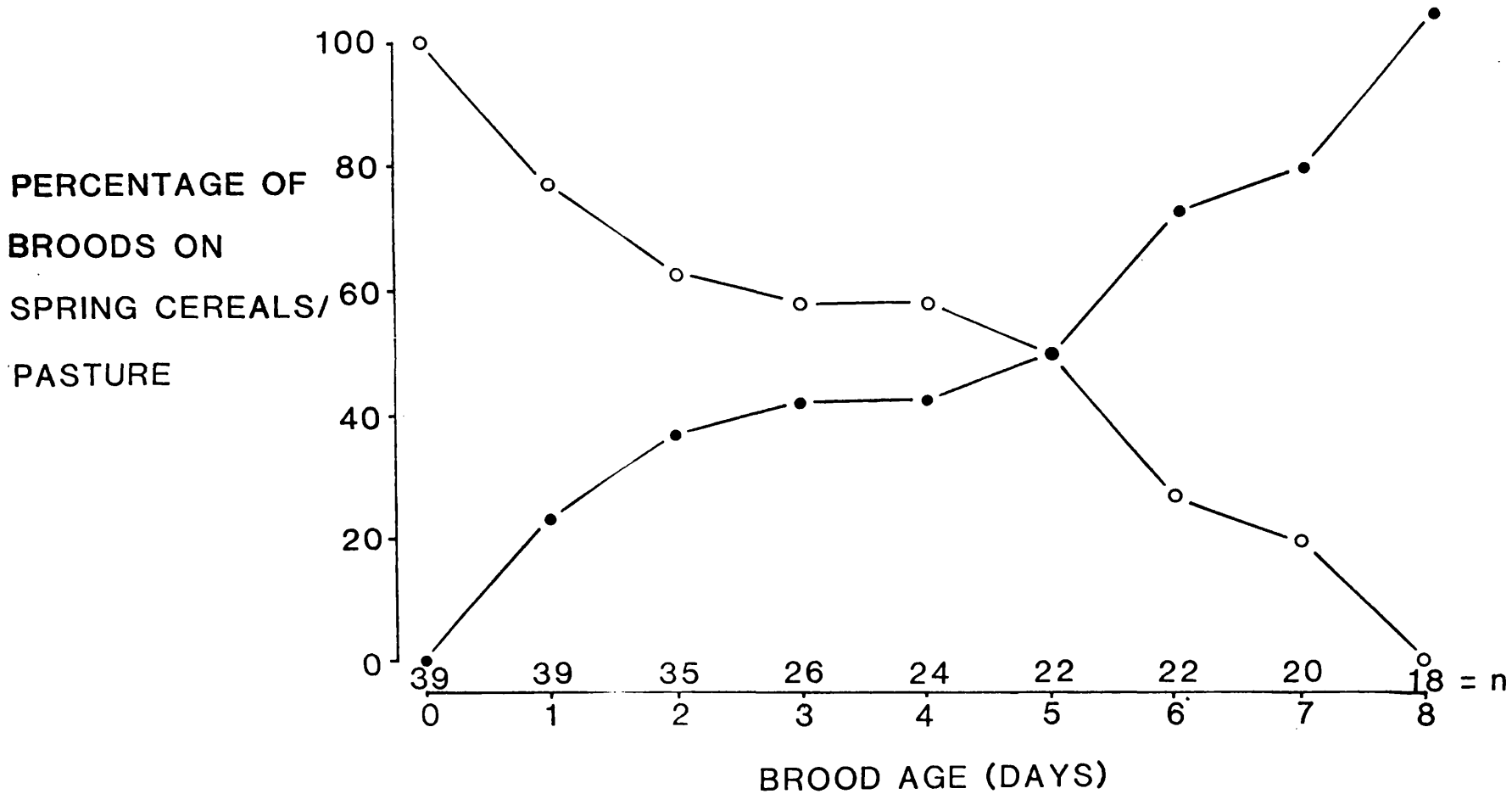

PERCENTAGE OF BROODS ON SPRING CEREALS/ PASTURE
100
80
60
40
20
0
39 39 35 26 24 22 22 20 18 = n
0 1 2 3 4 5 6 7 8
BROOD AGE (DAYS)

Figure 6.2

Habitat use by recently hatched broods of Lapwings on the rough grazing study area (all years combined). The three habitats comprise: unimproved (solid circles) and improved (triangles) rough grazing, and ditches and damp flushes (open circles).

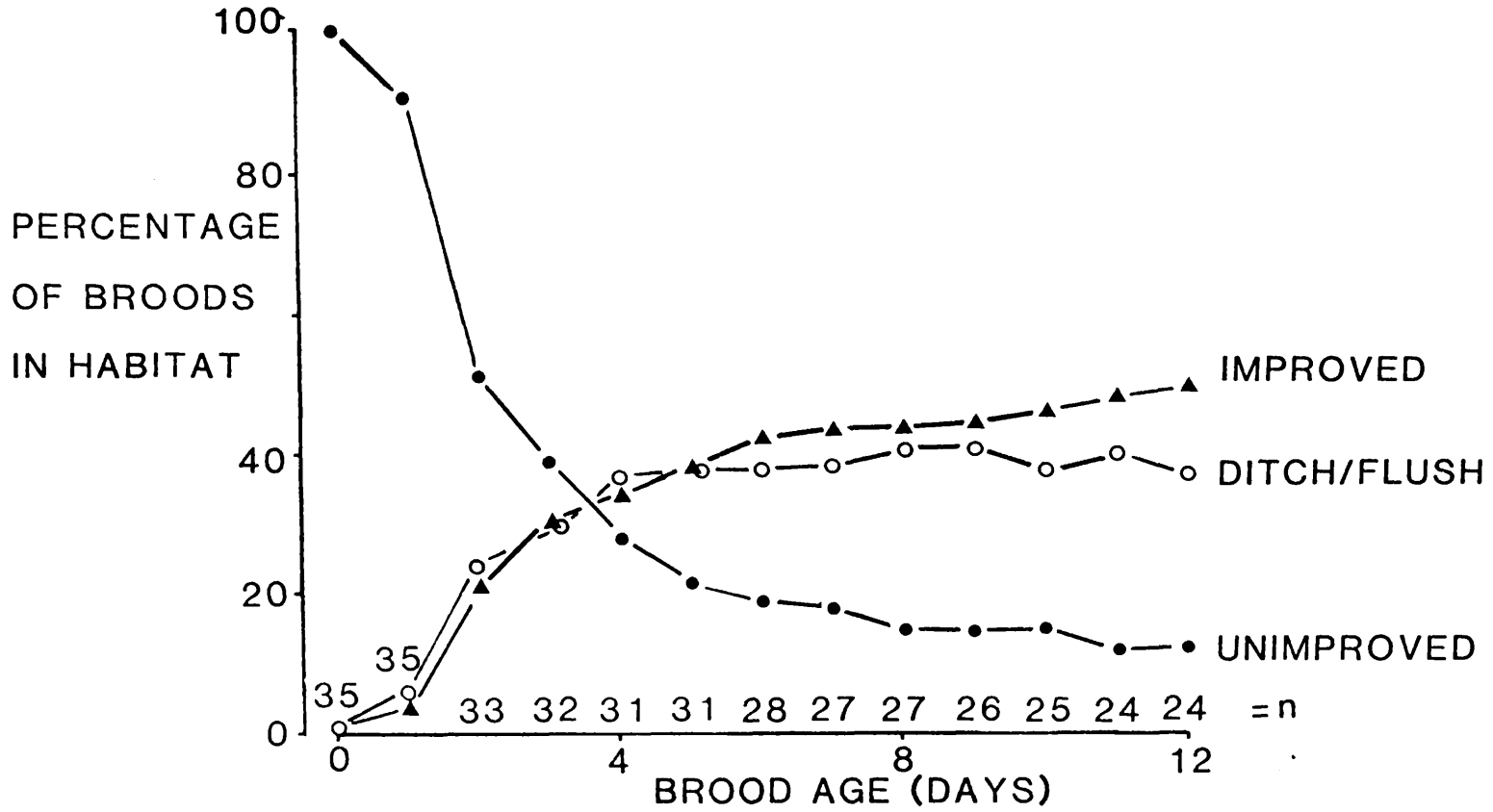

100
80
40
20
0
PERCENTAGE
OF BROODS
IN HABITAT
IMPROVED
DITCH/FLUSH
UNIMPROVED
35
35
33 32 31 31 28 27 27 26 25 24 24 =n
0
4
8
12
BROOD AGE (DAYS)

Figure 6.3

Grass height in 18 pasture fields on the arable study area and their use by lapwing broods.

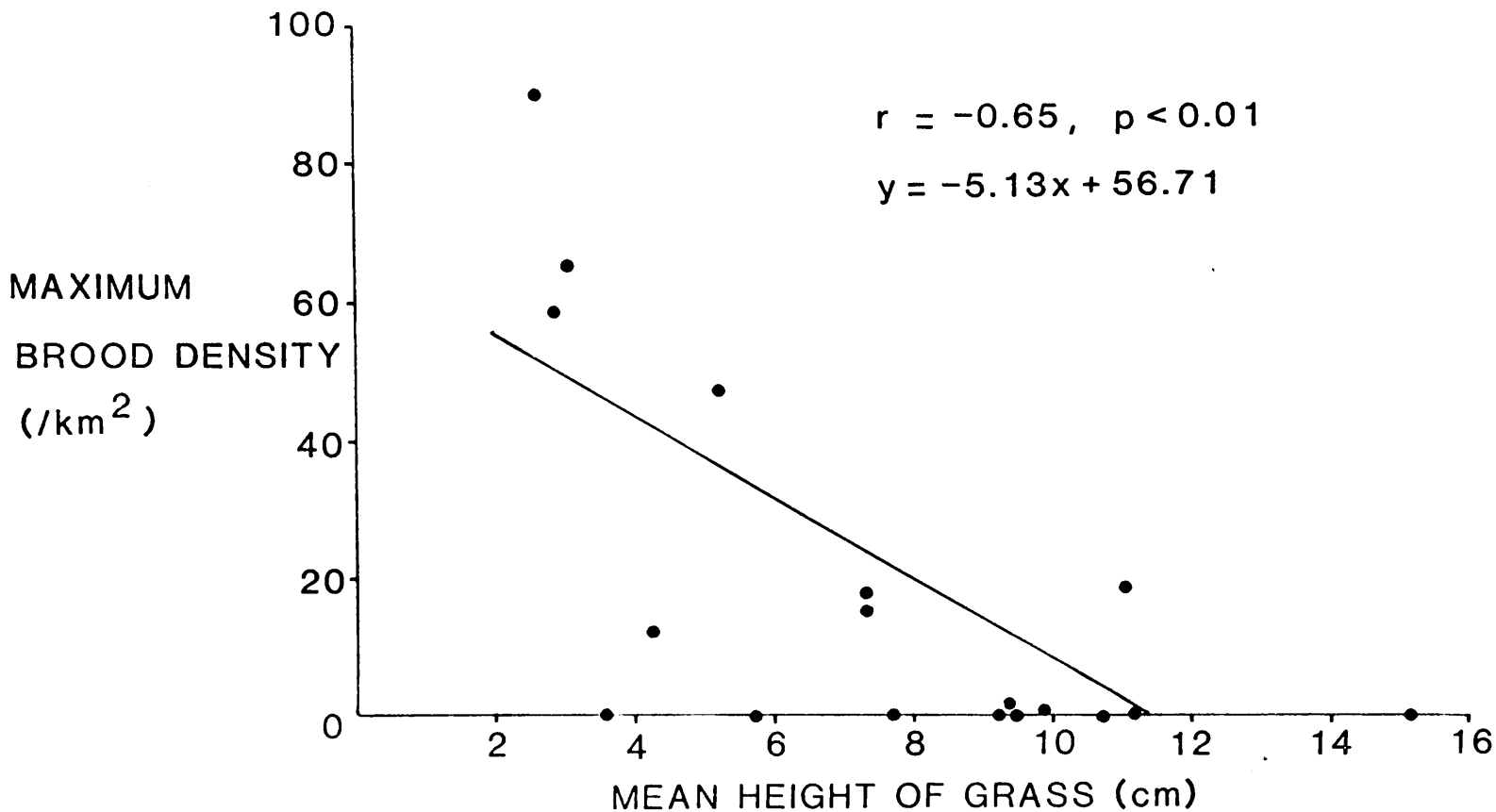

100
80
60
40
20
0
MAXIMUM
BROOD DENSITY
(/km2)
r = −0.65, p < 0.01
y = −5.13x + 56.71
2
4
6
8
10
12
14
16
MEAN HEIGHT OF GRASS (cm)

Figure 6.4

Habitat use by Lapwing broods on the arable site during 1986. Open and closed symbols refer to spring cereal and permanent pasture fields, respectively.

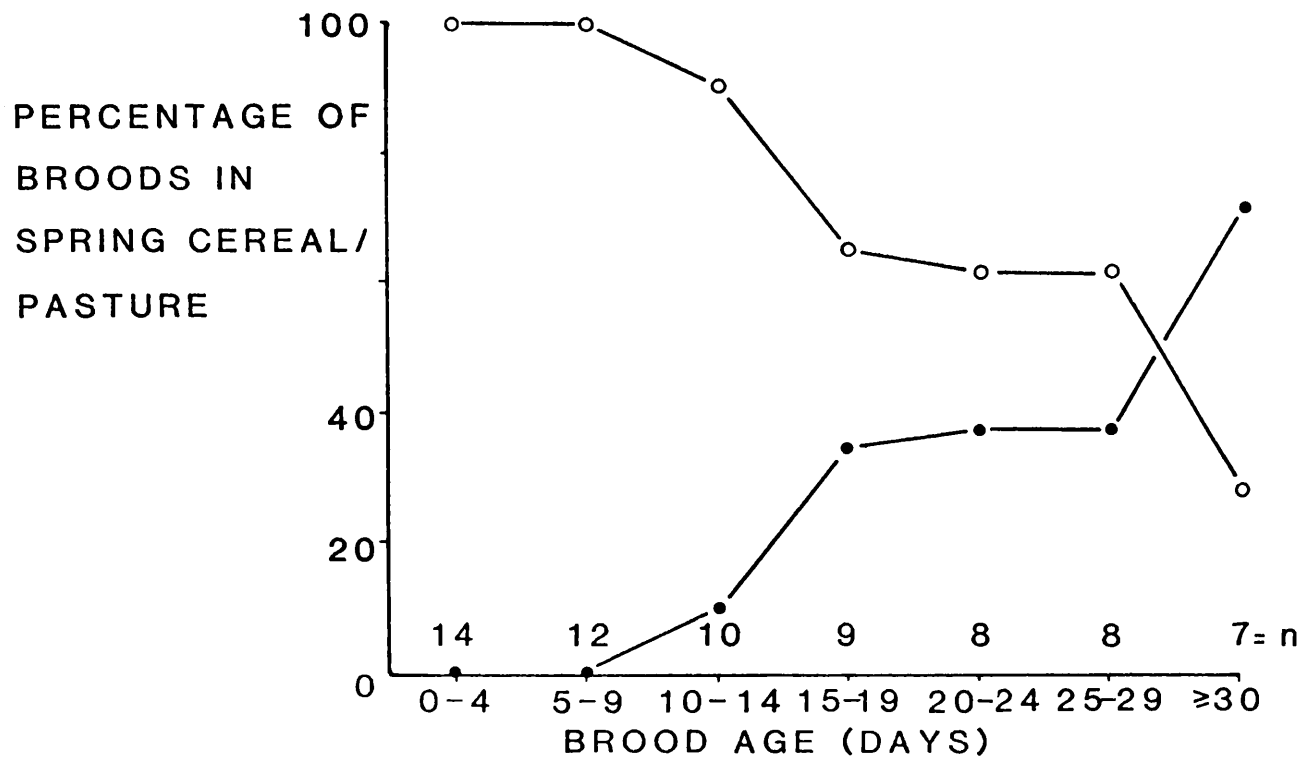

100
40
20
0
PERCENTAGE OF BROODS IN SPRING CEREAL/ PASTURE
14
12
10
9
8
8
7= n
0-4
5-9
10-14
15-19
20-24
25-29
≥30
BROOD AGE (DAYS)

Figure 6.5

Weight relative to age among Lapwing chicks from both the arable and rough grazing study areas combined. Vertical bars represent 95% confidence intervals. Data from 1984 and 1985.

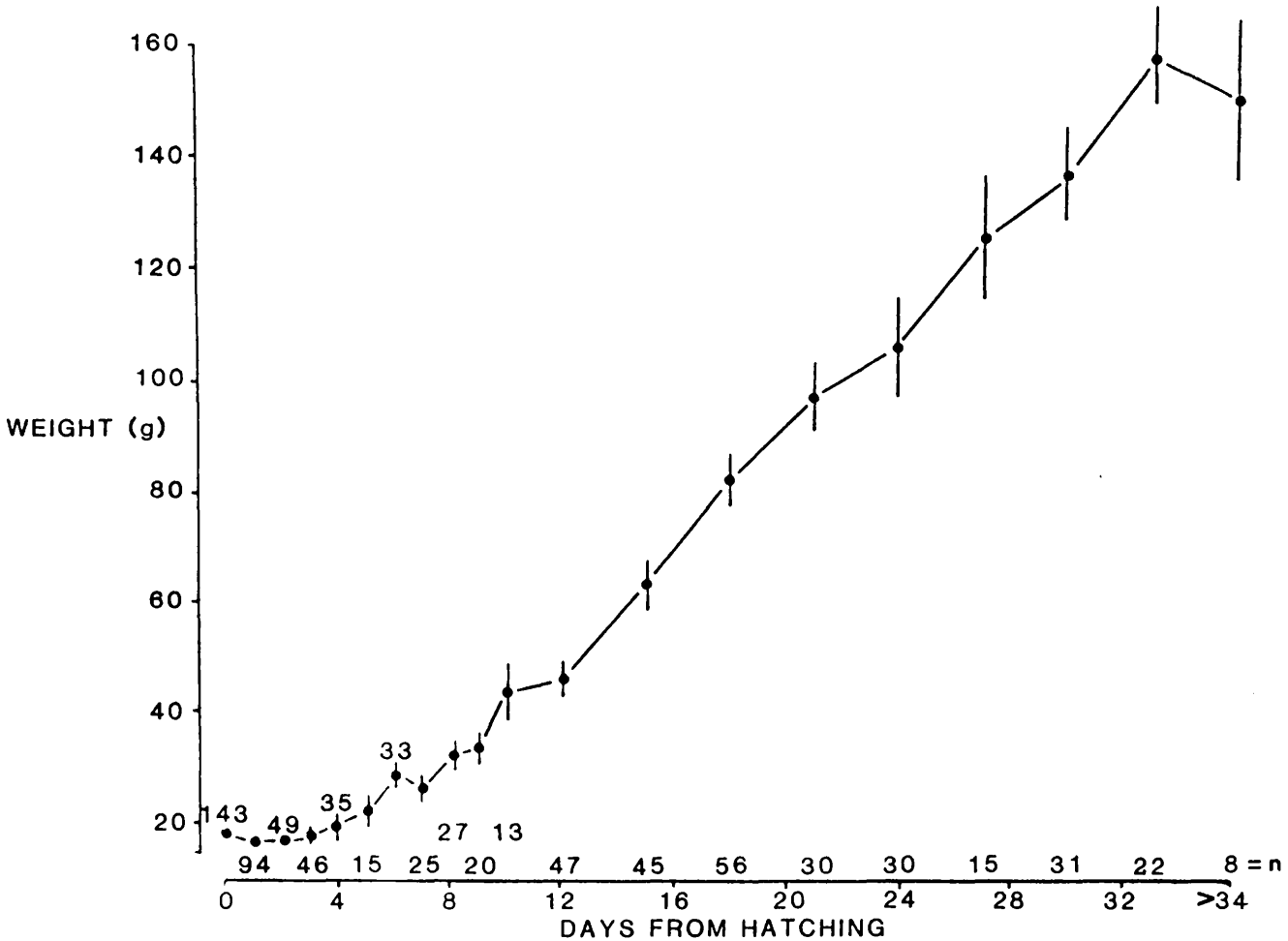

160
140
120
100
80
60
40
20
WEIGHT (g)
143
49
35
33
27
13
94
46
15
25
20
47
45
56
30
30
15
31
22
8 = n
0
4
8
12
16
20
24
28
32
>34
DAYS FROM HATCHING

Figure 6.6

Foot length relative to age among Lapwing chicks from both the arable and rough grazing study areas combined. Vertical bars represent 95% confidence intervals. Data from 1984 and 1985.

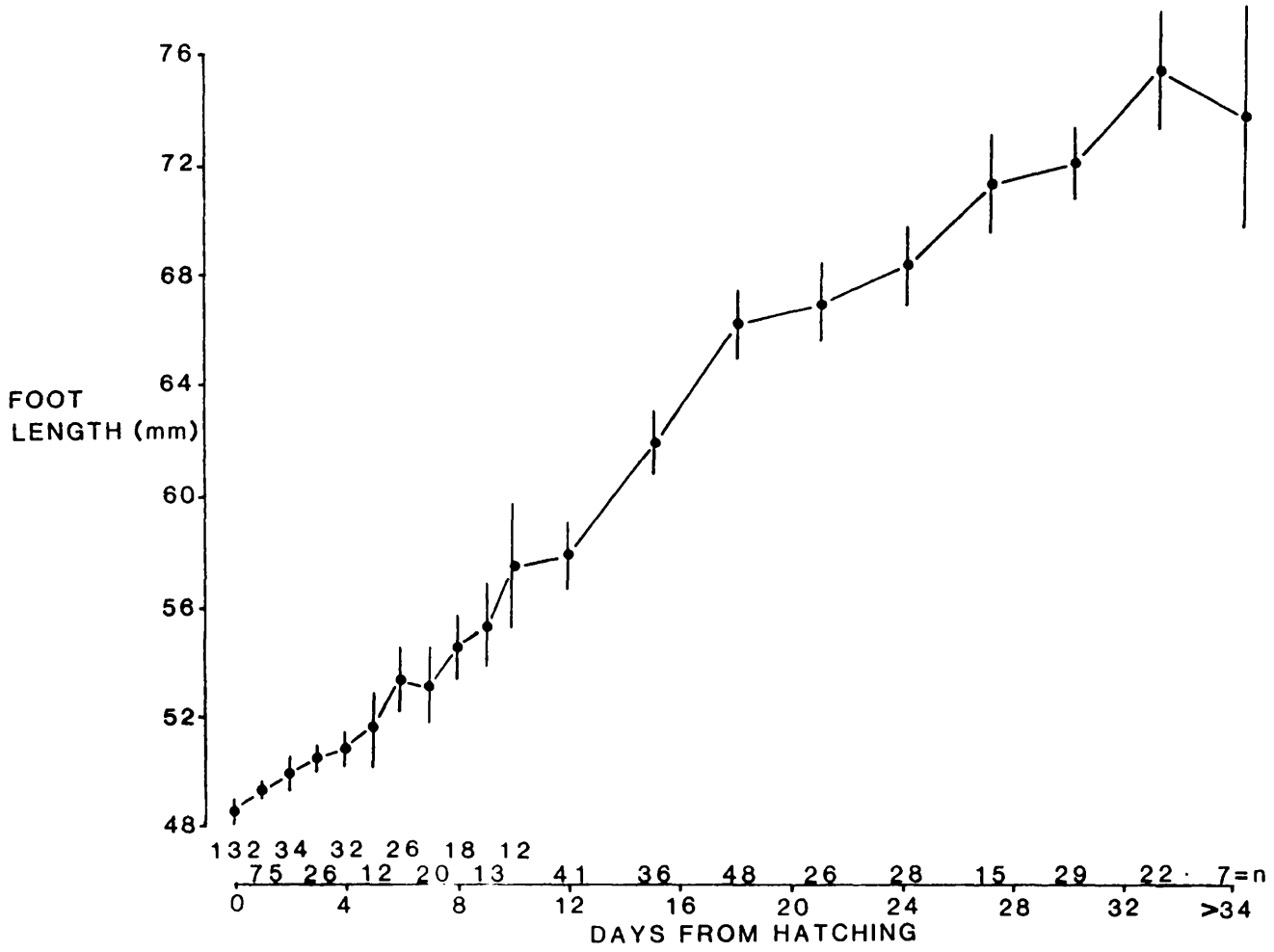

76
72
68
64
60
56
52
48
FOOT
LENGTH (mm)
132 34 32 26 18 12
75 26 12 20 13 41 36 48 26 28 15 29 22 7=n
0 4 8 12 16 20 24 28 32 >34
DAYS FROM HATCHING

Figure 6.7

Change in bill (open symbols) and head and bill length with age in Lapwing chicks from both the arable and rough grazing study areas combined. Vertical bars represent 95% confidence intervals. Data from 1984 and 1985.

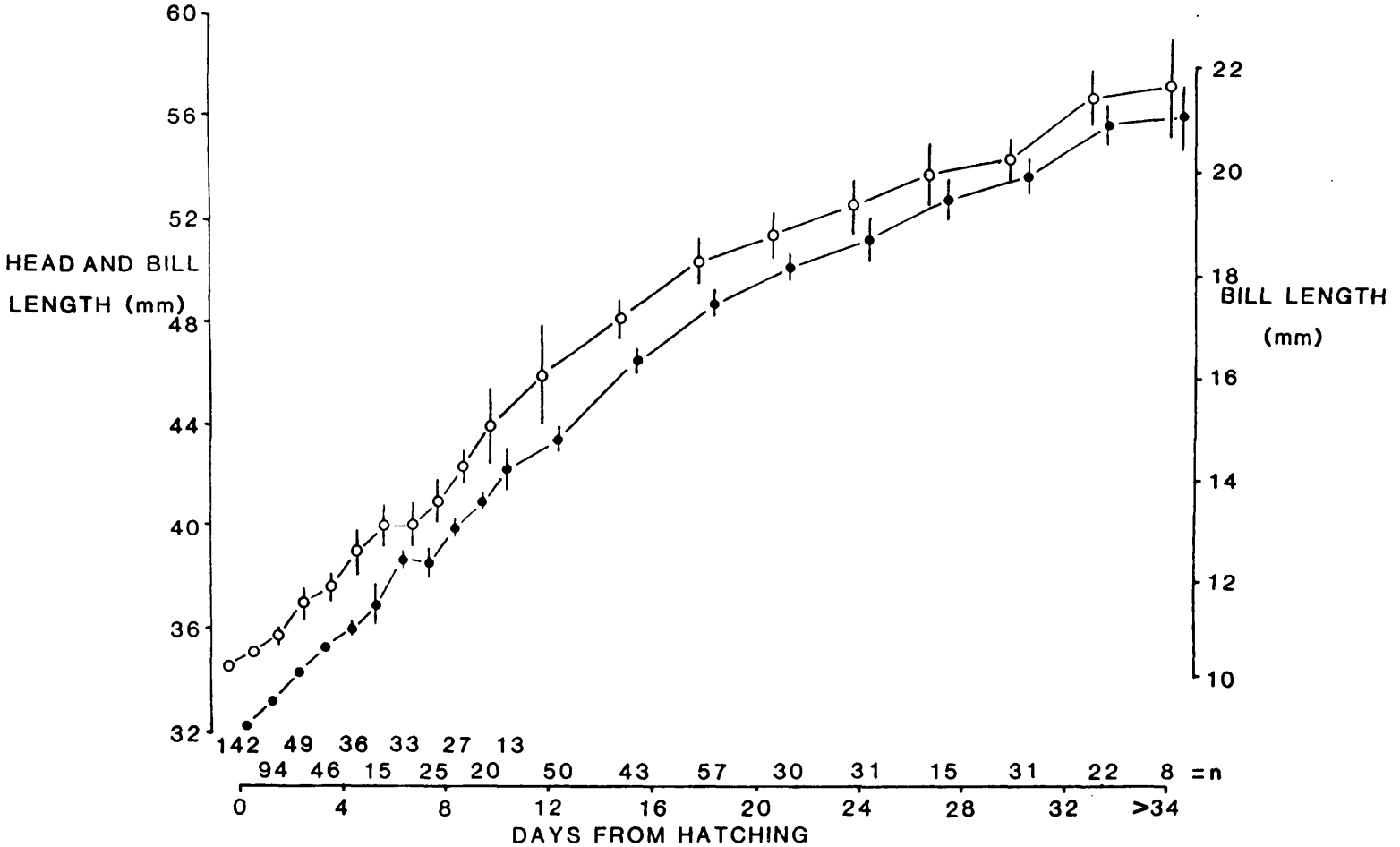

60
56
52
48
44
40
36
32
HEAD AND BILL
LENGTH (mm)
22
20
18
16
14
12
10
BILL LENGTH
(mm)
142 49 36 33 27 13
94 46 15 25 20 50 43 57 30 31 15 31 22 8 =n
0 4 8 12 16 20 24 28 32 >34
DAYS FROM HATCHING

Figure 6.8

Wing (closed symbols) and 9th primary length relative to age among lapwing chicks from both the arable and rough grazing study areas combined. Vertical bars represent 95% confidence intervals. Data from 1984 and 1985.

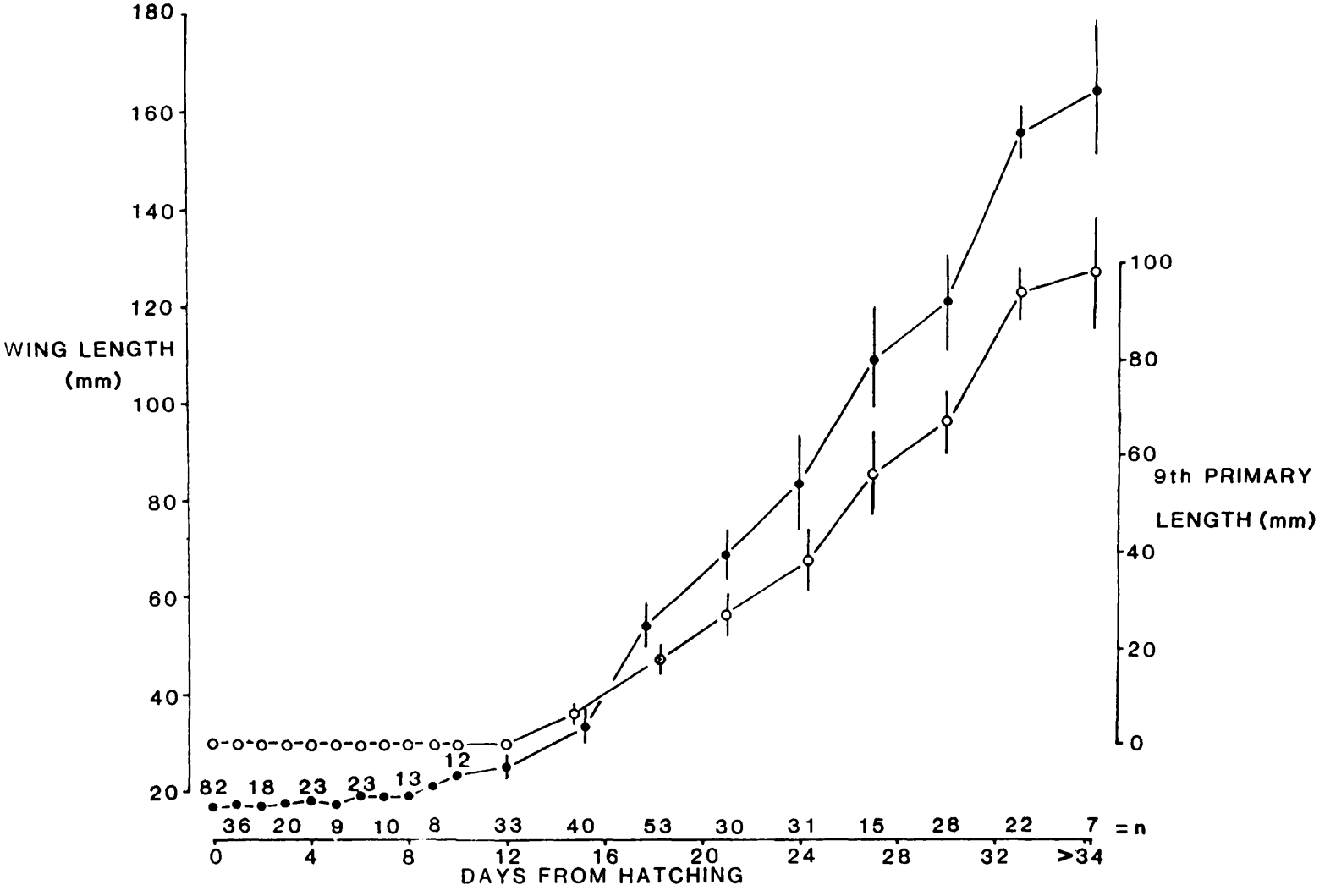

180
160
140
120
100
80
60
40
20
WING LENGTH
(mm)
100
80
60
40
20
0
9th PRIMARY
LENGTH (mm)
82 18 23 23 13 12
36 20 9 10 8 33 40 53 30 31 15 28 22 7 = n
0 4 8 12 16 20 24 28 32 >34
DAYS FROM HATCHING

Figure 6.9

Chick dimensions relative to adult size during the period from hatching to fledging. Data from 1984 and 1985.

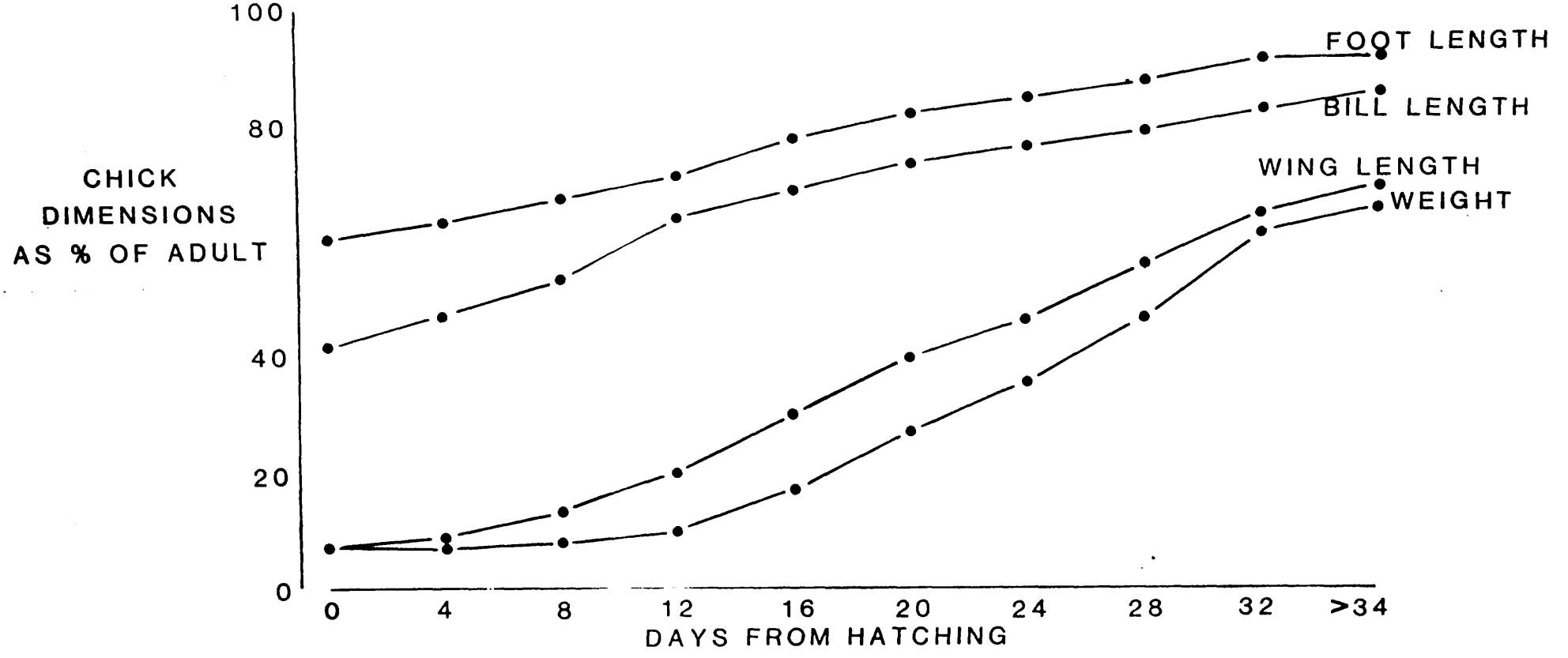

100
80
40
20
0
CHICK
DIMENSIONS
AS % OF ADULT
FOOT LENGTH
BILL LENGTH
WING LENGTH
WEIGHT
0
4
8
12
16
20
24
28
32
>34
DAYS FROM HATCHING

Figure 6.10

Chick weight (plotted on a logarithmic scale) relative to age on the arable (closed symbols) and rough grazing study areas. Data from 1984 and 1985.

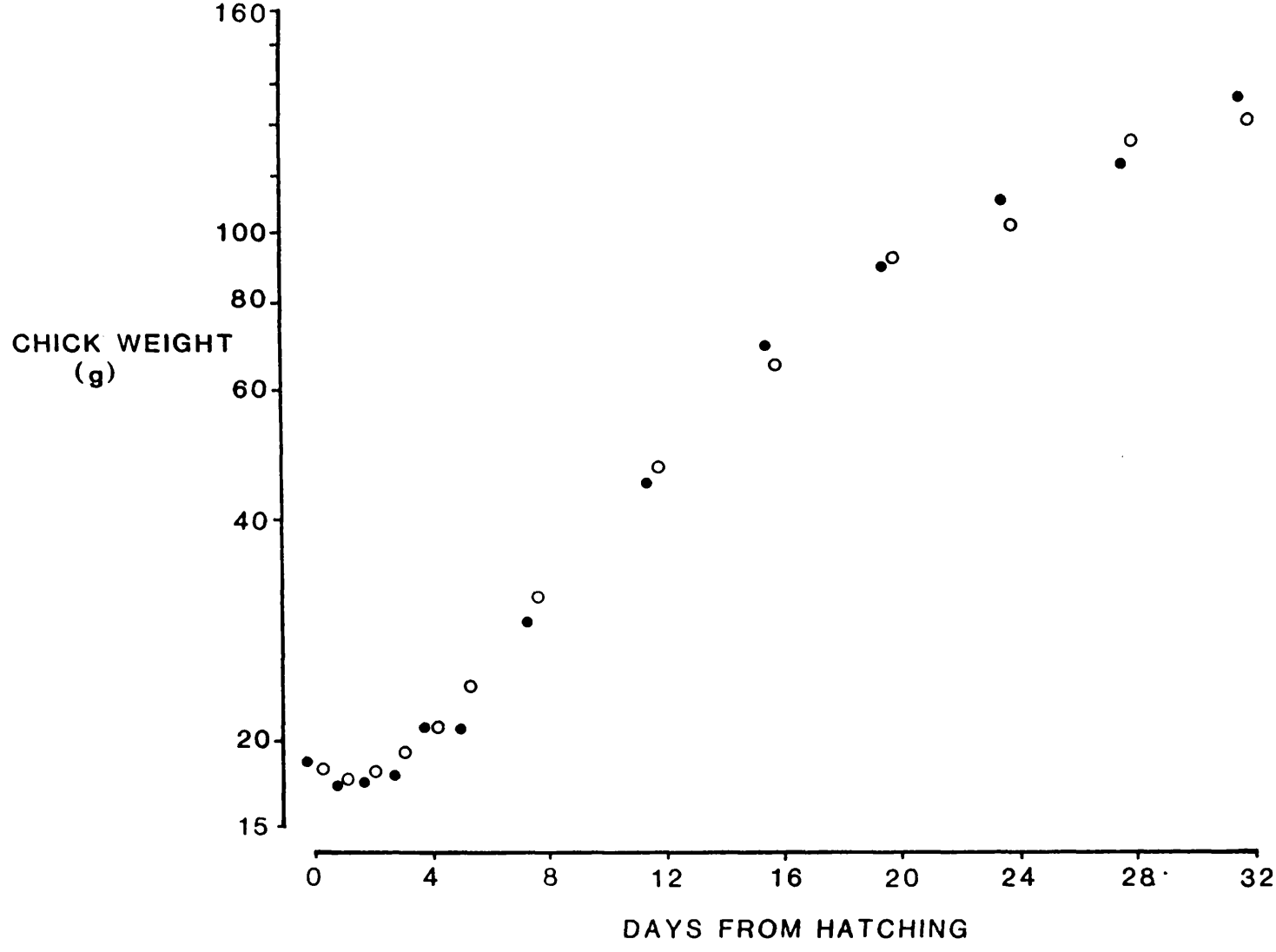

160
100
80
60
40
20
15
CHICK WEIGHT
(g)
0
4
8
12
16
20
24
28
32
DAYS FROM HATCHING

Figure 6.11

Chick head and bill length relative to age on the arable (closed symbols) and rough grazing study areas. Data from 1984 and 1985.

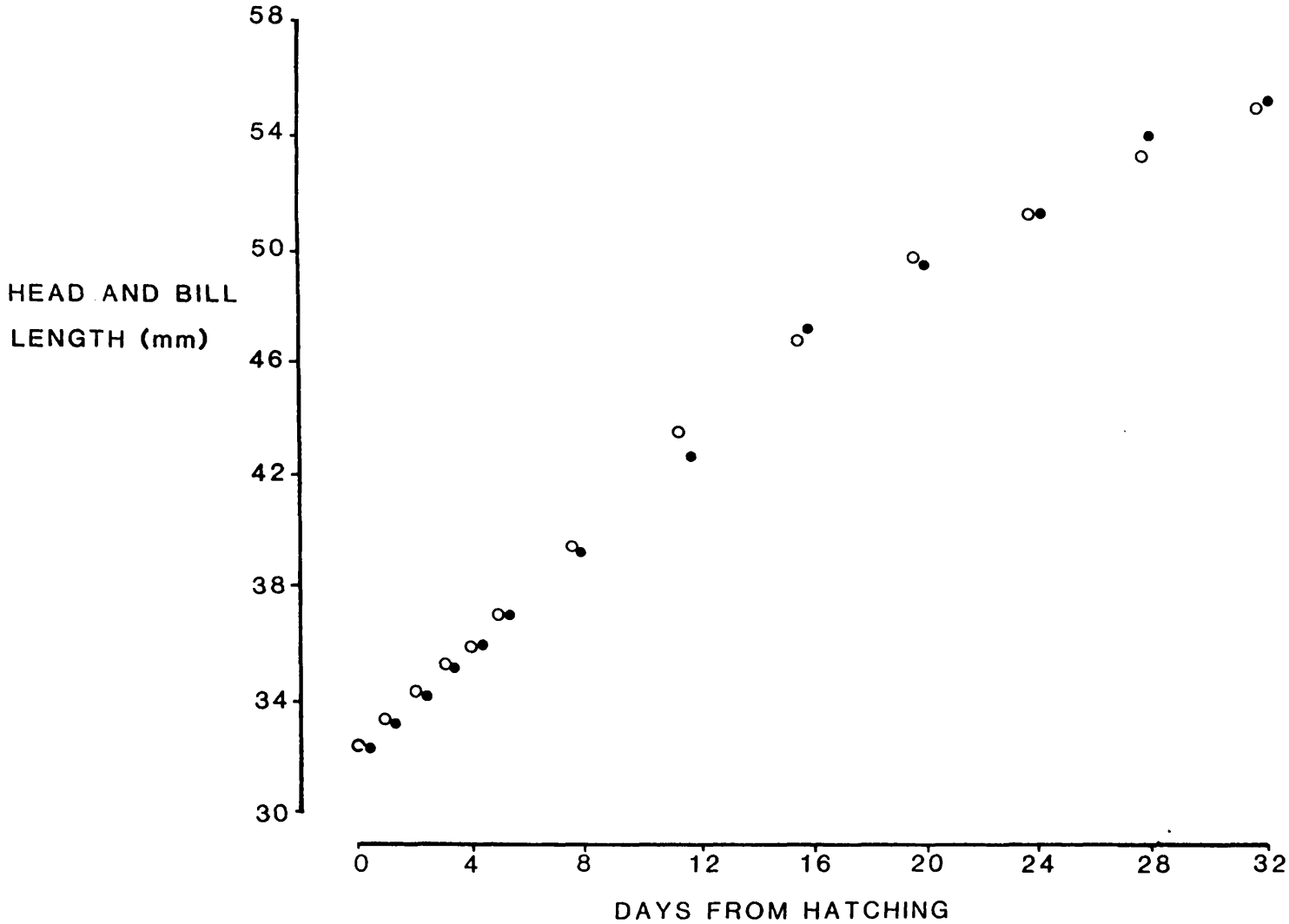

HEAD AND BILL
LENGTH (mm)
58
54
50
46
42
38
34
30
0
4
8
12
16
20
24
28
32
DAYS FROM HATCHING

Figure 6.12

Chick weight (plotted on a logarithmic scale) relative to age. Closed circles = the rough grazing study area; open and closed triangles refer to arable study area chicks which had moved from their natal spring cereal fields to pasture (open), and chicks which had failed to reach pasture and were still in cereal fields. Data from 1984 and 1985.

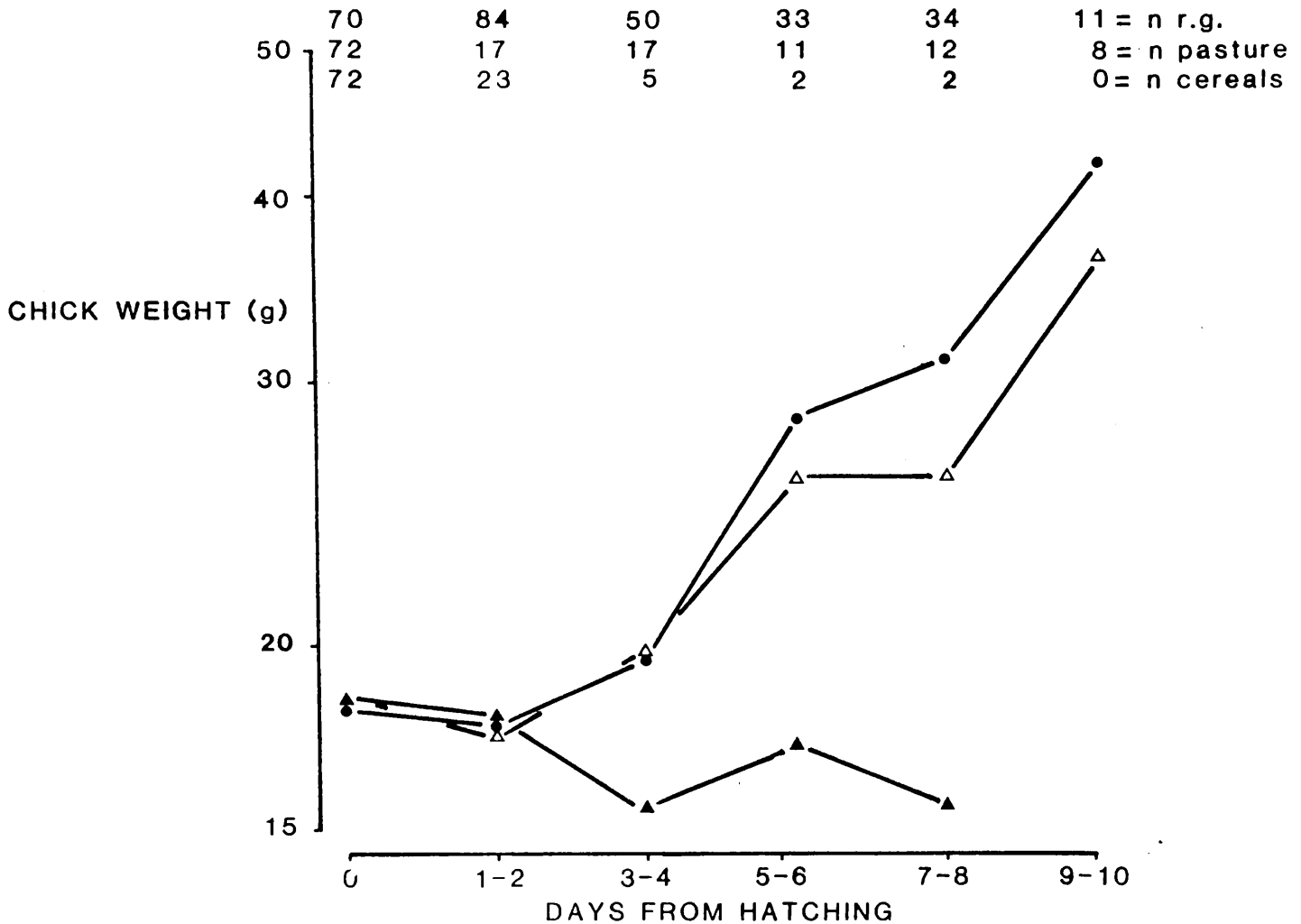

70 84 50 33 34 11 = n r.g.
50 72 17 17 11 12 8 = n pasture
72 23 5 2 2 0 = n cereals
CHICK WEIGHT (g)
50
40
30
20
15
0
1-2
3-4
5-6
7-8
9-10
DAYS FROM HATCHING

Figure 6.13

Chick head and bill length relative to age. Closed circles = chicks from the rough grazing study area; open and closed triangles are arable study area chicks which had moved from their natal spring cereal fields to pasture (open), and chicks which had failed to reach pasture and were still in cereal fields. Sample sizes as in Fig. 6.11. Data from 1984 and 1985.

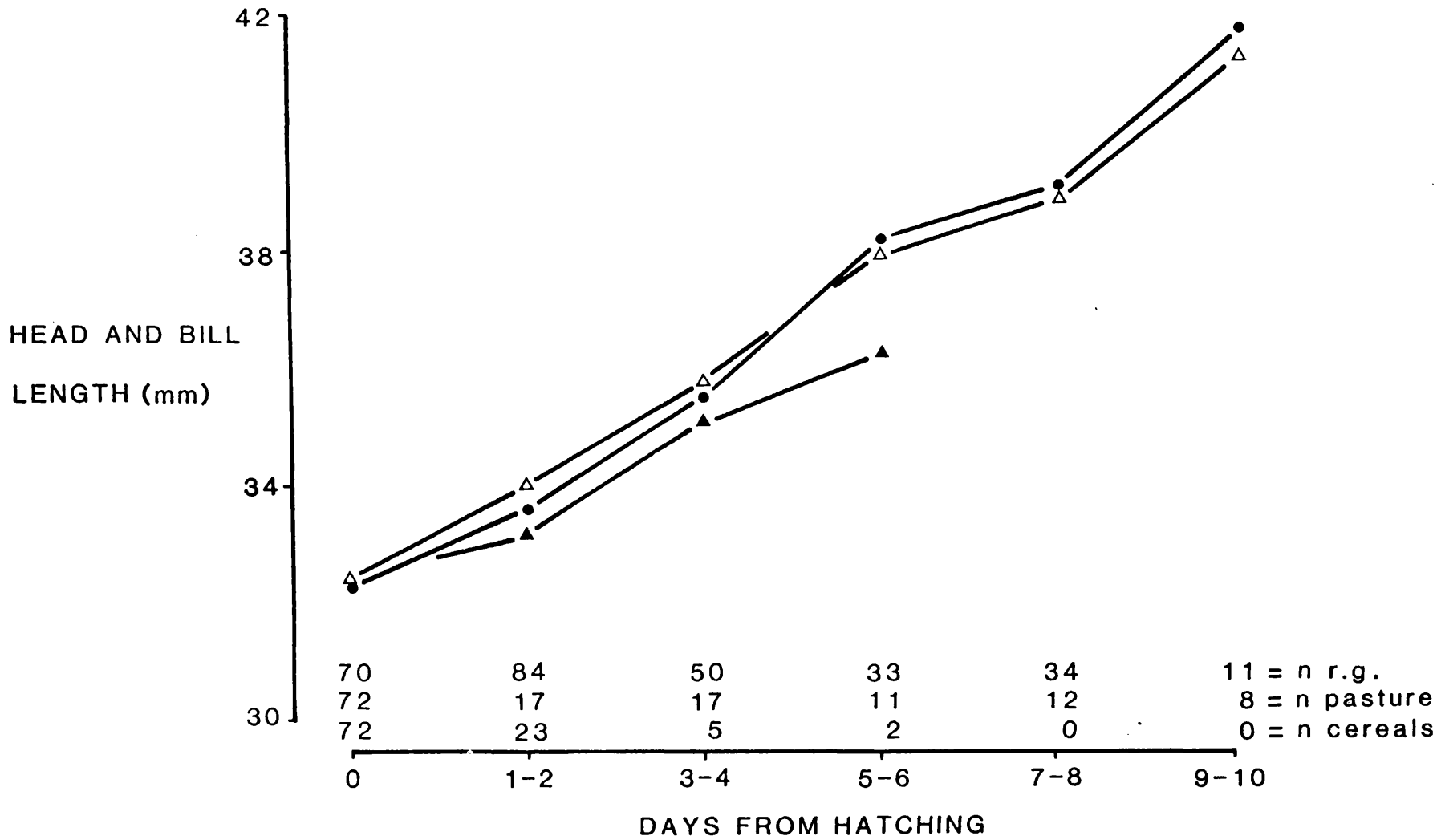

42
38
34
30
HEAD AND BILL
LENGTH (mm)
70 84 50 33 34 11 = n r.g.
72 17 17 11 12 8 = n pasture
72 23 5 2 0 0 = n cereals
0
1-2
3-4
5-6
7-8
9-10
DAYS FROM HATCHING

Figure 6.14

Chick body condition (weight/head and bill length) relative to age. Closed circles = chicks from the rough grazing study area; open and closed triangles are arable study area chicks which had moved from their natal spring cereal fields to pasture (open), and chicks which had failed to reach pasture and were still in cereals. Sample sizes as in Fig. 6.11. Data from 1984 and 1985.

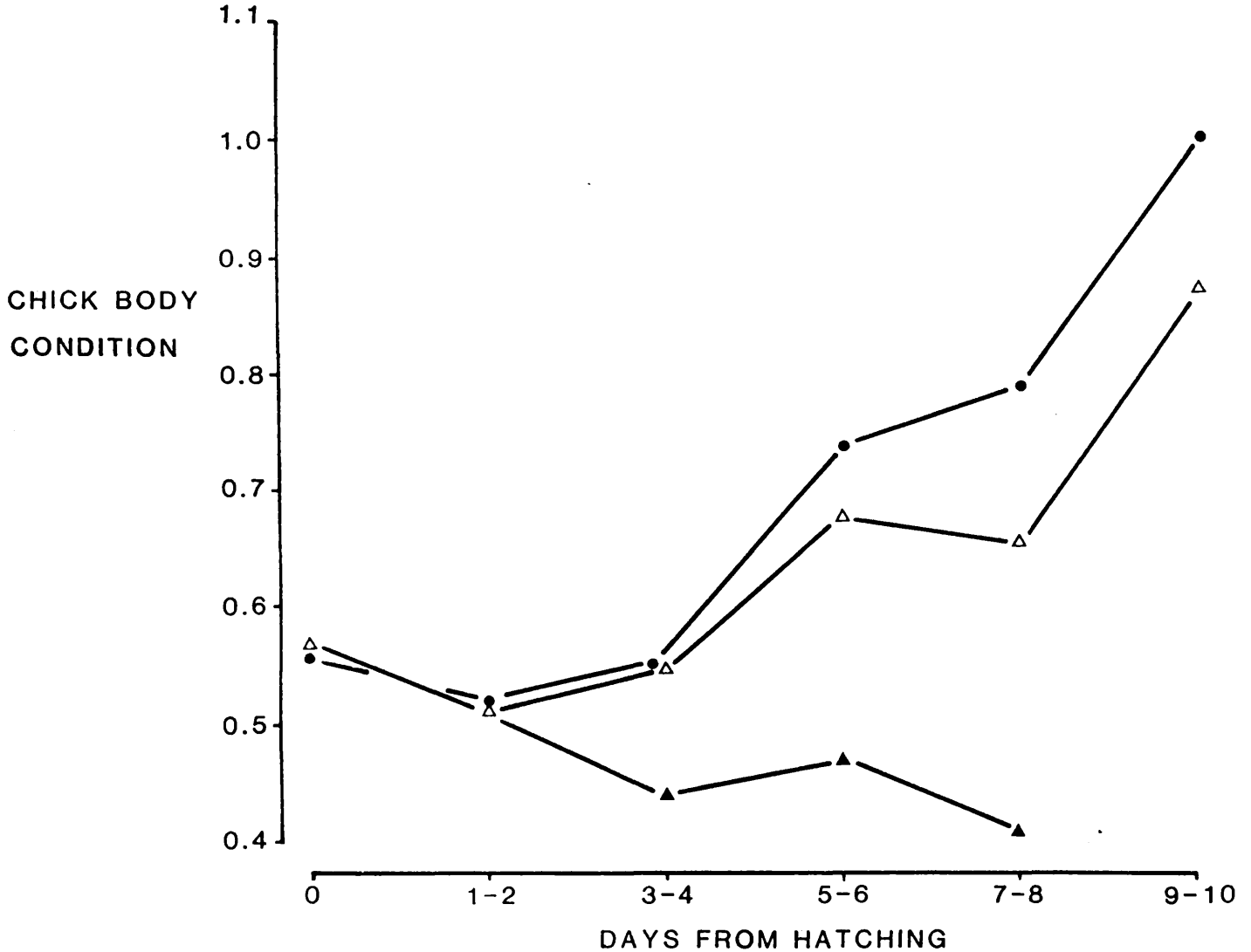
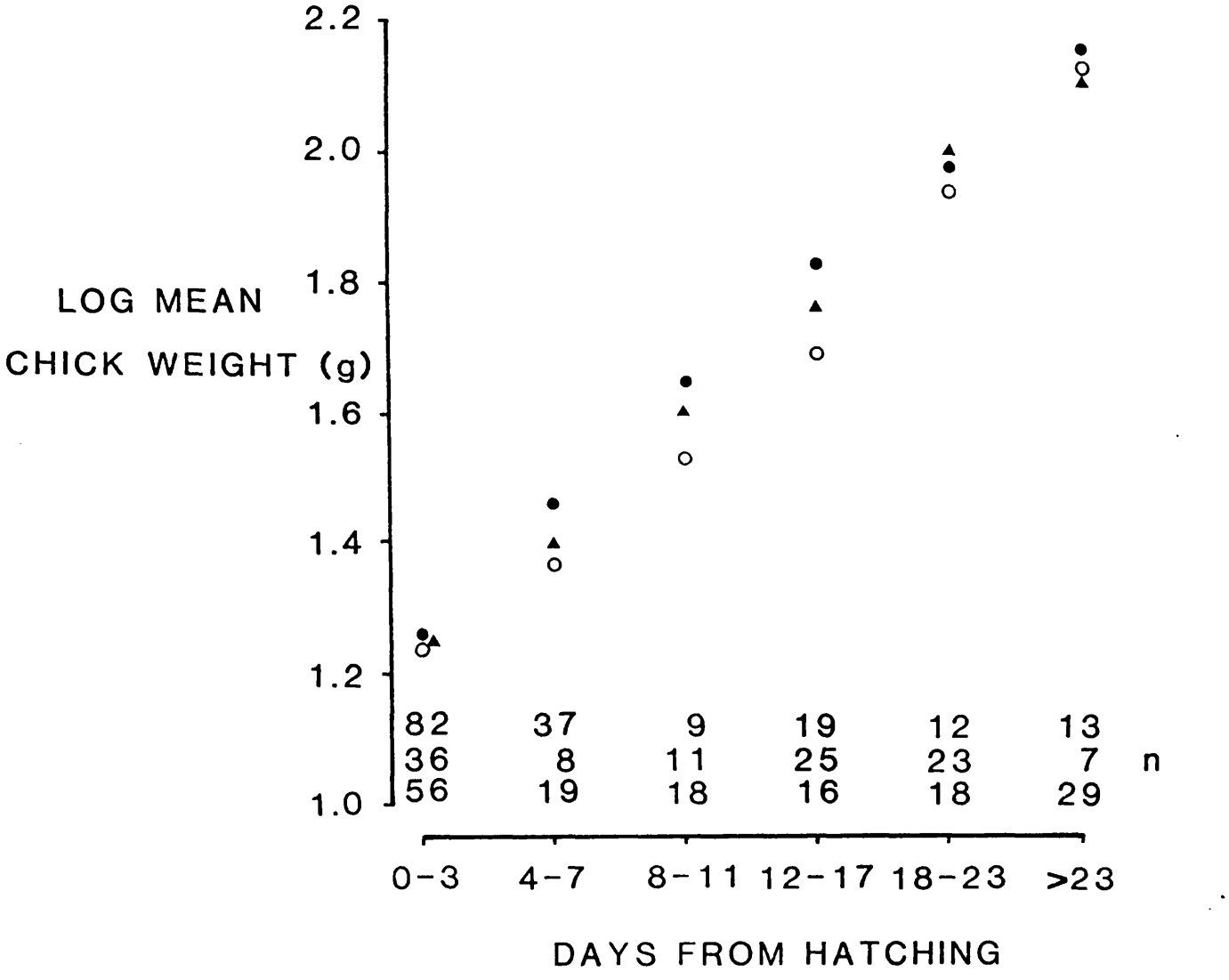

CHICK BODY CONDITION
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0
1-2
3-4
5-6
7-8
9-10
DAYS FROM HATCHING

Figure 6.15

Mean chick weight (plotted on a logarithmic scale) relative to age on the rough grazing study area. Closed circles = early chicks (hatched before 9th May); closed triangles = middle chicks (hatched between 9th and 29th May); open circles = late chicks (hatched after 29th May). Data from 1984 and 1985.


LOG MEAN
CHICK WEIGHT (g)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
82 37 9 19 12 13
36 8 11 25 23 7 n
56 19 18 16 18 29
0-3 4-7 8-11 12-17 18-23 >23
DAYS FROM HATCHING

Chapter 7. THE POPULATION EFFECTS OF TERRITORIALITY.

7.1 INTRODUCTION

Territorial limitation of population density has been shown to have potentially important consequences for avian population dynamics (e.g Glas 1960, Watson 1967, Zimmerman 1971, Charles 1972, Klomp 1972, O'Connor 1980, Patterson 1980). Formal models linking behaviour, habitat quality and population processes were initially proposed by Brown (1969) and Fretwell and Lucas (1970) - their "ideal despotic model". As applied to breeding territories, this latter model predicts that colonists will first occupy the habitat in which their breeding success will be highest. By acting despotically, these initial colonists will impose a limit to the carrying capacity of the habitat, beyond which point further potential settlers will be forced to colonise suboptimal habitats where their breeding density and success will be lower. Eventually, after a succession of progressively poorer quality habitats have been filled, some birds may refrain from breeding altogether, forming a non-breeding surplus. By causing an increasing proportion of the total population to refrain from breeding and/or colonise habitats where their productivity is not sufficient to make good the losses incurred due to mortality, this process might act as a density dependent brake on population increase. In either event the net effect will be that overall breeding success will be inversely related to population size. The degree of regulation actually imposed by this process will be a function of the magnitude of the differences in habitat suitability, together with the strength of any density independent factors acting on the population.

Two previous studies have suggested that territorial limitation of breeding density might occur in wader populations. Through removal experiments, Holmes (1970) and Harris (1970) demonstrated that

surpluses of potential breeders apparently exist among Alaskan Dunlin and Welsh Oystercatchers, respectively. When breeding birds were removed, their territories were quickly re-occupied by birds from the non-breeding surplus. Both authors considered that their evidence demonstrated the existence of behavioural limitation of population density. Their conclusions have, however, been contested by Evans and Pienkowski (1984) on two specific points: it is claimed that neither study conclusively proved that the re-occupants of the artificially vacated territories might not have bred elsewhere if they had not been encouraged to settle in the study areas (it is difficult to imagine, however, how this could be demonstrated not to be the case). Secondly, they question the general applicability of the Oystercatcher study, which took place on a small island, to the mainland population which is currently expanding into new habitats. Evans and Pienkowski (1984) considered it unproven that regulation occurs in wader populations and that it is more likely that they are kept below the "utopian level" at which it might occur by the action of density independent factors.

During the first year of this study it became apparent that there were differences in the timing of occupation, breeding density and success between rough grazing sites. These were investigated in greater detail during the subsequent two seasons to assess their importance, if any, in population regulation.

7.2 METHODS

The techniques used in the investigation of hatching and fledging success have already been described (Chapter 5). The pattern of territory occupation by males was investigated by censussing displaying birds as often as weather conditions allowed. All censusses were carried out during fine weather and in the early morning, when display activity was most intense. Censussing began as soon as birds

returned from their winter quarters and ended when most birds had layed. Nest density was quantified using nearest neighbour distances (Clark and Evans 1954), obtained by pacing out the distance between closest pairs of concurrent nests.

7.3 RESULTS

Nesting density, numbers and territory occupation.

There were significant differences in nesting density between the three rough grazing sites. Nest density was highest at Kepp, intermediate at Balafark and lowest at Gribloch (Table 7.1).

Table 7.1. Mean nearest neighbour distances on the three rough grazing sites (all three years combined).

	n Nests	MEAN NEAREST NEIGHBOUR DISTANCE (m)	s.d.	
KEPP	91	43.6	26.118	
				z = -7.34,p<0.001
BALAFARK	48	112.7	60.113	
				z = 1.88,p<0.05
GRIBLOCH	11	183.8	172.891	

The timing of territory occupation by males also differed between sites (Fig. 7.1). In both years when detailed censusses were carried out, occupation began first on the Kepp site, followed by Balafark and then Gribloch (except in the final year when Gribloch was not occupied at all). In spite of being occupied later, there was little difference in the timing of laying of first clutches on the three sites (median first egg dates: Kepp 6th April; Balafark 6th April; Gribloch 9th April).

The overall rough grazing study populations of displaying males during the three study years are shown in Table 7.2. During the first two years the population was constant. In the third year, however, there was a marked reduction in numbers. The reasons for this

reduction are not known but could have been due to a high mortality of adults in wintering areas in France, Ireland and south-west England during the preceeding winter (British Trust for Ornithology pers comm.). The percentage decrease between 1985 and 1986 was greatest at Gribloch and least at Kepp (Table 7.2).

Table 7.2. Numbers of displaying male Lapwings on the three rough grazing sites during the three study years.

	n DISPLAYING MALES		
	1984	1985(% CHANGE)	1986(% CHANGE)
KEPP	26	27(+3.8)	23(-14.8)
BALAFARK	22	24(+9.0)	15(-37.5)
GRIBLOCH	5	4(-20.0)	0(-100)

Breeding success.

There were no significant differences in hatching success between the three sites (Table 7.3). However, whereas fledging success and productivity were similar at Kepp and Balafark (Table 7.4), they were significantly lower at Gribloch (X^2 tests comparing numbers of chicks which survived or which died: Kepp/Balafark = 2.11, n.s; Kepp+Balafark/Gribloch = 4.23, $p<0.05$)

Table 7.3. Nest survival on the three rough grazing sites. p is the daily survival probability, v^2 its variance, and t was calculated from $p^1 - p^2 / \sqrt{v_1^2 + v_2^2}$ (Hensler and Nicholls 1981). Hatch success is the percentage of nests which hatched at least one egg ($p^{32} \times 100$).

	p	v^2	HATCH SUCCESS	
KEPP	0.964	2.6×10^{-5}	31.1	
				t = 0.914, n.s
GRIBLOCH	0.975	1.2×10^{-4}	45.1	
				t = 0.399, n.s
BALAFARK	0.970	3.7×10^{-5}	38.0	

Table 7.4. Fledging success and productivity (chicks fledged/female) on the three rough grazing study areas (all three years combined).

	n FEMALES	n CHICKS DIED	n CHICKS FLEDGED(%)	PRODUCTIVITY
KEPP	38	118	34 (22.3)	0.9
BALAFARK	26	58	26 (30.9)	1.0
GRIBLOCH	9	19	1 (5.0)	0.1

The reasons for the lower fledging success at Gribloch are not known. However, the Gribloch habitat was more homogenous in that the unimproved rough grazing was broken up by fewer improved areas (the % area of improved land was approximately 9%, compared with 19% at Balafark and 24% at Kepp). This meant the chicks having to move further to suitable feeding areas (the mean distance between the Gribloch nests and improved feeding areas was 83m, compared with only 26m at Kepp), which might have resulted in a higher early mortality. Alternatively, predation might have been heavier, or the adults which bred on the Gribloch site may have been younger, less experienced or of lower quality than those which bred elsewhere on the rough grazing.

7.4 DISCUSSION

There were marked differences in the timing of occupation, breeding density and success between the rough grazing sites. The site in which productivity was lowest (Gribloch) was occupied latest in the season and at a lower density than the other two sites. Furthermore. in the final year of the study, when breeding numbers were generally low, this site suffered the greatest proportional reduction in numbers. Although the Kepp and Balafark sites also differed (although to a lesser extent) in the timing of occupation and breeding density, no significant differences in breeding success were detected. This

could be due to these two sites being too similar in suitability for any relatively minor productivity differences to be detectable.

These results conform to the predictions of the "ideal despotic model" (Fretwell and Lucas 1970) and suggest that a behavioural mechanism may exist whereby at least some Lapwing populations might be regulated. Conclusive proof for the existence of such a mechanism could only be provided by many more years of observations on population size and productivity and/or experimental manipulation of population density. However, by making various assumptions from the three years data which are available, it is possible to derive a tentative measurement of the strength of the putative density dependent relationship.

Varley and Gradwell (1960) showed that the strength of density dependence can be measured using Key factor Analysis. When the k factors (the log number of organisms surviving a particular stage of their life cycle minus the log number which entered that stage, i.e the k factor is a measure of the intensity of mortality) are plotted against population size, a positive slope which is significantly greater than zero indicates that a density dependent mortality factor is acting. Too few data are available to carry out this procedure empirically. However, by using the breeding performance parameters obtained during the three study years (Table 7.5), and by assuming that: a) polygyny is restricted to a small minority of males; b) a maximum of 50 "pairs" will be able to establish themselves in the Kepp and Balafark sites; c) any birds unable to establish themselves will colonise Gribloch or sites of similar quality, the possible strength of density dependence can be modelled. The parameters used in the construction of the model are shown in Table 7.6.

Table 7.5. Breeding performance parameters on the three rough grazing sites (all three years combined).

	n FEMALES	n EGGS LAYED	n FLEDGLINGS	EGGS/ FEMALE	FLEDGLINGS/ FEMALE
BALAFARK+KEPP	64	336	60	5.25	0.93
GRIBLOCH	9	40	1	4.44	0.11

Table 7.6. Parameters used in construction of population model. n eggs and n fledglings calculated using data in Table 7.5 and assuming that a maximum of 50 females can nest on the Kepp and Balafark sites and that any further colonists will be forced to nest at Gribloch or an equivalent site.

POPULATION SIZE (FEMALES)	n EGGS	LOG n EGGS	n FLEDGLINGS	LOG n FLEDGLINGS	k
50	262	2.418	46.5	1.667	0.75
60	307	2.487	47.6	1.678	0.81
80	396	2.597	49.8	1.697	0.90
100	484	2.685	52.0	1.716	0.97
120	573	2.758	54.2	1.734	1.02
140	662	2.821	56.4	1.751	1.07
160	751	2.876	58.6	1.768	1.11
180	840	2.924	60.8	1.784	1.14
200	929	2.968	63.0	1.800	1.17

When the k values in Table 7.6 are plotted against log n eggs the resulting regression coefficient is 0.763, suggesting a strongly density dependent effect. As Varley and Gradwell (1960) pointed out, the two axes in this regression are not independent (log n eggs is being plotted against log n fledglings - log n eggs) and the resulting regression coefficient can only be accepted as valid if plots of log n eggs against log n fledglings and vice versa give regression coefficients which are significantly different from unity. This was

the case in the present analysis (b = 0.239 with 95% confidence limits of 0.027; b = 4.096 with 95% confidence limits of 0.465, respectively).

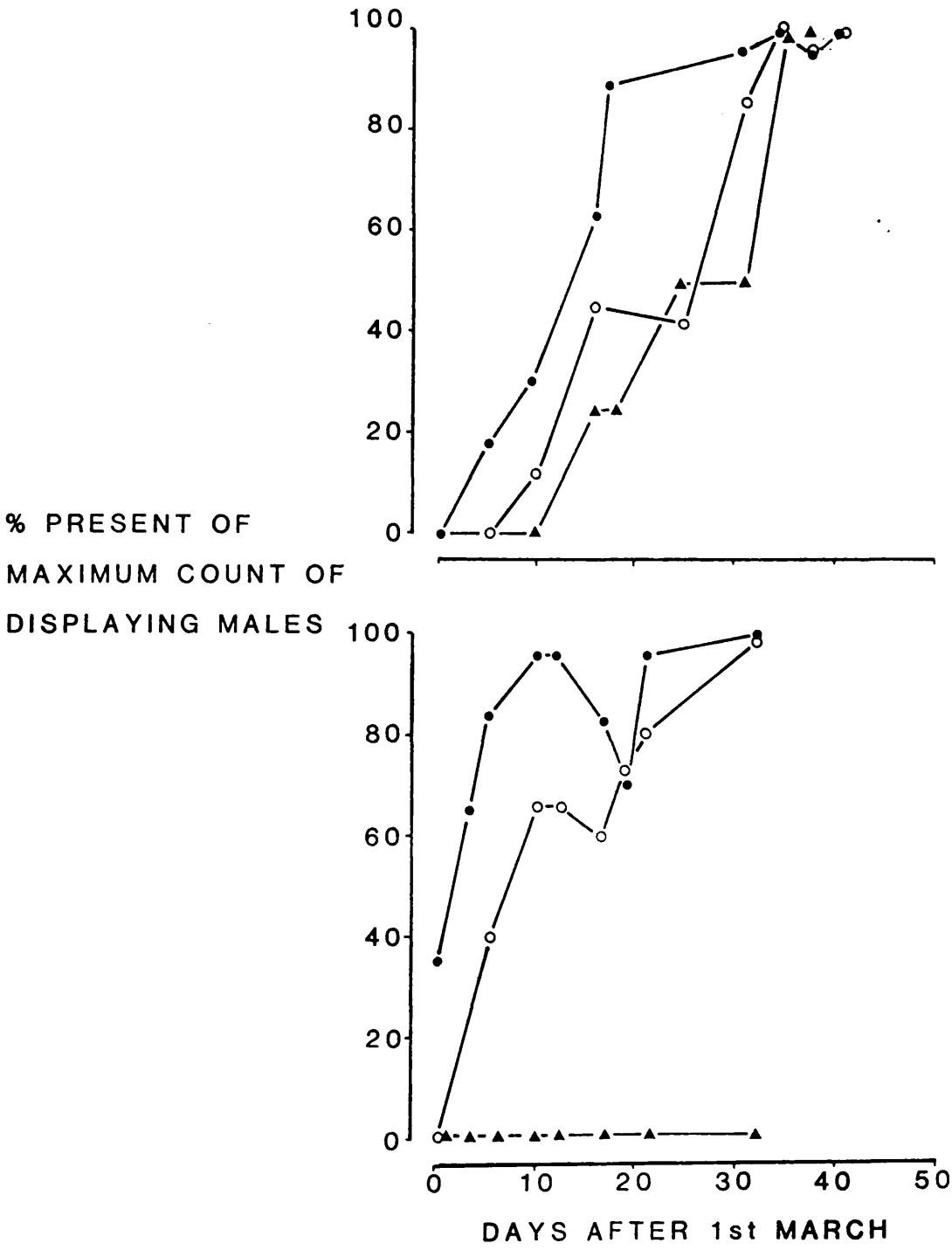
It is important to realise that this model is based on a limited data set and is realistic only if the assumptions outlined above are met. Given only three years observations and only a small number of individually marked males, it is not possible to be certain that 50 is indeed the maximum population which can breed on the two best sites, that excluded birds may not find alternative sites which are of better quality than Gribloch, or that polygyny is uncommon enough to be safely ignored.

A further complicating factor in the interpretation of population size and productivity trends is that density independent factors (such as weather) which may cause birds to refrain from breeding and so influence population density, might also reduce mean breeding success. In 1986, for example, inclement weather in the early part of the season may have been at least partly responsible for the population reduction on the rough grazing site. In that year the rough grazing breeding success was the lowest recorded (Chapter 5), perhaps because of the weather. Thus, density independent factors might act to complicate analyses based on between year comparisons. Ideally, the effects of weather should be controlled for by carrying out within year comparisons between a number of sites with different breeding densities (either naturally occurring or manipulated).

At best, these results suggest that territoriality might play a role in the regulation of at least some Lapwing populations. Further intensive and, more importantly, experimental field work is needed to confirm this.

Figure 7.1

Pattern of territory occupation by displaying males on the three rough grazing study areas during 1985 (upper) and 1986. Closed circles = Kepp; open circles = Balafark; closed triangles = Gribloch.


% PRESENT OF
MAXIMUM COUNT OF
DISPLAYING MALES
100
80
60
40
20
0
0
10
20
30
40
50
DAYS AFTER 1st MARCH

Chapter 8. GENERAL DISCUSSION

Agriculture and Lapwings

Throughout their breeding range, Lapwings are primarily farmland birds. Before the climax forests of Europe were felled and replaced with agricultural land, Lapwings may have been largely confined to the steppes and semi-deserts of eastern Europe and Asia. By replacing forest with steppe-like land, man created new habitats to which Lapwings were pre-adapted and which they successfully colonised. The success of their adaptation to the agricultural habitat is evidenced by their abundance and widespread distribution throughout the once afforested areas of the northern Palearctic.

This study has shown that virtually all aspects of Lapwing breeding ecology are sensitive to agricultural land-use patterns: crop type and growth rate and field size and the timing and intensity of cultivation influence the feeding behaviour of the adults and chicks, nesting habitat selection, hatching and fledging success and chick growth and movements. By being able to adapt to mans' activities to this extent, Lapwings have been successful in that they are probably much commoner than they once were and they have greatly extended their range. Evolutionary change, however, takes place comparatively slowly and there is a danger that the rapidity with which contemporary agricultural patterns and processes are changing will prove detrimental to present Lapwing populations.

The rapidity and scale of recent agricultural change has been greatest on arable land (Chapter 1) and it is in this habitat that Lapwing breeding success has been affected most by land-use policy. In two of the study years, hatching success, the length of the laying season and chick survival were all reduced to the point where productivity was insufficient to compensate for adult and juvenile

mortality. In the third year, the pattern was different only because abnormal weather conditions upset the usual pattern of cultivation and crop growth. Three other studies have shown that Lapwings breeding on intensively farmed arable land elsewhere in Europe have a reduced breeding success compared to Lapwings breeding on marshland or rough grazings (Beser and Helden-Sarnowski 1982, Kooiker 1984 and Matter 1982). Egg losses during cultivation and poor chick survival were cited as the main factors responsible for low productivity in all three studies.

In spite of their poor reproductive performance, Lapwings are widespread on British arable farmland and their breeding densities there are high (Nicholson 1938, Galbraith et al. 1984). Why do they persist on arable land when the penalties are so high? There are three possible explanations:

a) the birds breeding on the arable farmland may be "overspill" from the fully occupied rough grazing. Although there is competition for the better rough grazing sites (Chapter 7), it is unlikely that the large numbers of birds which breed on arable land are simply displaced. Lapwings are known to show comparatively little natal philopatry (Mead et al. 1968). However, in spite of the large number of chicks colour marked in both study areas, there was no instance of one returning to breed outwith its natal habitat. Also, if exclusion from the rough grazing into the arable was occurring, we might expect the latter to become occupied only after the former. This was not the case; both study areas were occupied virtually simultaneously.

b) certain short-term benefits might be gained from nesting on arable land. It has already been shown that egg and, perhaps, chick predation was less severe on the arable site (Chapters 4 and 5).

Access to high quality feeding habitat is another way in which adult Lapwings might benefit from nesting on arable farmland. The prey

biomass on permanent pasture far exceeds that on improved rough grazing and lapwing feeding success was higher there. Because of this, maternal body condition was better among female Lapwings nesting on arable land and they produced larger eggs. Eggs in replacement clutches on the rough grazing site were smaller than those in first clutches but this was not the case on the arable site. This suggests that not only are feeding conditions initially better on the arable land, but that any seasonal deterioration in food availability is less severe. If anthropogenic factors had not reduced chick survival, the hatchlings from these larger eggs should have had an enhanced survival.

Since the evolutionary "pay off" of any behavioural or morphological trait is ultimately in terms of the number of offspring reared, and, since productivity on the arable site was low, it is difficult to see how such short-term benefits alone could account for the continued existence of the large numbers of birds which breed on arable farmland.

c) arable farmland may have been more suitable as a nesting habitat in the past but has recently become less so. This study has shown that the poor breeding success of Lapwings on the arable site was partly due to the rapid growth of cereals. This shortened the breeding season and forced the chicks to undertake hazardous journeys to permanent pasture where they were not dwarfed by the vegetation. Whether or not the chicks had easy access to pasture fields was a major determinant of their survival. Thus, the growth characteristics of the cereal crops and the distribution and accessibility of pasture were important influences on Lapwing breeding performance.

From conversations with the local farmers it became apparent that the habitat mixture on the arable site had changed greatly over the previous 10-15 years. The local changes that occurred match those

which have characterised British arable farming as a whole, with a reduction in the amount of livestock and pasture and an increased emphasis on cereal production. Whereas, during the three years of the study pasture comprised about 19% of the total land under crops, 15 years previously it comprised about 50%; hay and cereals made up the remainder. As pasture fields were ploughed and replaced with cereals, the amount of suitable nesting habitat increased, but easy access from those fields to pasture is likely to have become more restricted.

In addition to more land being sown with cereals, the nature of the cereal crop itself has changed over the last decade or so: traditional varieties of crop have been replaced with strains which are more tolerant of crowding, disease and pest resistant, and faster growing. This has encouraged farmers to sow the individual seeds closer together, thus producing an earlier and denser crop with fewer bare patches. The result of this is likely to be that modern cereal fields are more impenetrable and less hospitable habitats for Lapwing broods than they once were. The harsh weather in 1986 simulated the earlier situation by slowing down crop growth and creating bare patches in the fields and it is interesting that chicks were then able to remain in their natal cereal fields and survived as well as rough grazing chicks.

According to the local farmers, Lapwings were commoner and more widespread within the arable area before the reduction in pasture occurred. When the present study began in 1984 there were 162 displaying males counted on the arable site. This had decreased to 132 in the following year and to 98 in 1986. The 26% reduction between 1985 and 1986 was matched by a 30% reduction on the rough grazing site and may have been due to a high mortality during the previous winter (Chapter 7). The reduction between 1984 and 1985 did not, however, occur on the rough grazing site, indicating that a decrease in numbers

in response to habitat change might be taking place. By analysing the British Trust for Ornithology's Common Bird Census data, O'Connor and Shrubb (in press) found that habitat-induced population changes were occurring elsewhere in Britain. In those English counties in which pasture has been replaced by cereals, the Lapwing populations have declined. In neighbouring counties where no such changes have occurred, the Lapwing numbers are stable. Interestingly, they also found that Lapwing numbers have been reduced in counties where autumn-sown have largely replaced spring sown-cereals. On the arable site, also, Lapwings showed a substantial but non-significant preference for spring cereals over autumn-sown cereals. Again the timing of crop growth could be the important determinant in habitat choice. Autumn cereals may be a less suitable nesting habitat since they are generally about 10 cm higner throughout their spring growth than spring cereals.

It may be that the attraction of short-term benefits in the comparative scarcity of predators and better feeding conditions, together with the recent nature of the habitat changes that have occurred, explain the continued existence of lapwings on the arable site. If so, the situation is unstable and further population reductions might be expected to occur, especially if the current trend toward the replacement of pasture with cereals continues.

If the low productivity found in the arable population in this study applies generally throughout British arable farmland, then the conservation of rough grazing Lapwings becomes especially important. The removal of this productive component of the overall population, through the drainage and improvement of their nesting habitat, could have unlooked for consequences outwith the rough grazing habitat.

Population regulation in waders

This study has demonstrated that Lapwing populations may be at least partly regulated through their social behaviour during the breeding season. By acting despotically, male Lapwings may impose a limit to the carrying capacity of their breeding areas and exclude sub-dominant birds to less suitable areas where their productivity is low. With only three years observations it is not possible to be sure beyond a reasonable doubt that this results in population limitation, however, the results suggest this and at least indicate the value of looking for breeding season regulation in wader populations. Clearly, we need to understand if and how wader population sizes are regulated, if the effects of changes in agricultural land use are to be related to wader numbers, dynamics and, ultimately, conservation.

In spite of the evidence of removal experiments (Harris 1970, Holmes 1970), Evans and Pienkowski (1984) doubted that wader populations are regulated at all and argued that density independent factors keep their numbers below the level at which density dependent regulatory factors might begin to act. Goss-Custard (1981), however, accepted that density dependent processes might operate during the breeding season and showed that they, together with a slight density dependent winter mortality, could regulate populations. The degree of regulation would depend on the strength of the density dependent relationships in comparison with any density independent factors.

If wader populations are not regulated and behave in the manner claimed by Evans and Pienkowski (1984), then they should exhibit marked and erratic fluctuations from year to year, as essentially random density independent factors exert their effect. If such changes occur and are to be detected, then, ideally, regular censusses of entire geographical populations of waders would have to be carried out. During the breeding season, when the birds are widely dispersed

and difficult to census, such an undertaking would be impractical. In the winter, however, many waders concentrate into relatively few estuaries, and censussing is much simpler.

Regular extensive counts of the waders wintering on U.K. estuaries have been carried out since 1971 (results summarised in Prater 1981, and Salmon and Moser 1985). These counts show that whereas some species are remarkably consistent in their midwinter population levels or display very limited year to year variation, others are more variable (Table 8.1), (these data should be treated with caution, since it is possible that the midwinter count in any one year might be affected by large-scale effluxes or influxes to the U.K. due to severe weather. Thus the year to year variability within the U.K. could be affected by the ability of that particular species to tolerate narsh weather conditions. Also, because of its relatively mild winter weather, the U.K. might be a particularly favoured winter area and occupied preferentially. If this were so, the variability shown in the counts might not be a true reflection of the actual annual variations in population levels (since, when populations are low, birds which might have otherwise wintered elsewhere move into the U.K.)).

Notwithstanding the above reservations, the wide variation in the data presented in Table 8.1 raises several interesting questions: are some populations entirely unregulated; are some regulated more than others and, if so, why?

Table 8.1. The mean year to year percentage change, regardless of sign, in the January indices for 10 wader species censussed annually in the U.K. between 1971 and 1985. The breeding areas have been classified climatically as either arctic or temperate. Census data from Salmon and Moser (1985).

	MEAN PERCENT CHANGE	BREEDING AREA
SANDERLING	43.2	ARCTIC
KNOT	27.3	"
BAR-TAILED GODWIT	26.1	"
GREY PLOVER	19.2	"
CURLEW	18.8	TEMPERATE
RINGED PLOVER	15.7	"
REDSHANK	13.2	"
TURNSTONE	12.1	ARCTIC
DUNLIN	11.1	TEMPERATE/ARCTIC
OYSTERCATCHER	10.0	TEMPERATE

The greatest degree of year to year variation occurs mainly in species which breed in the arctic (Table 8.1). Those which breed in more temperate areas generally display less variation. This apparent difference can be at least partly explained by reference to the possible severity of density independent factors operating during the migration and breeding seasons. The timing of the snow-melt and weather exert important and highly variable density independent effects on wader breeding success in arctic regions (Green et al. 1977). Such effects might be expected to mask any density dependent factors which might be operating. Weather effects on breeding success in temperate areas will be less dramatic and density dependent factors able to exert a stronger regulatory control, hence the more limited year to year changes in Table 8.1. Thus, the question, whether wader populations may be regulated on their breeding areas, might over-

simplify a complex situation by ignoring the possibility that the mix of density independent and dependent factors (and, therefore, their net effect) might vary between species with different geographical ranges, and even between different populations of the same species. Furthermore, social behaviour during the breeding season varies widely between different species of waders, from monogamy and overdispersion to promiscuity and lekking (Pitelka et al. 1974). Given such a diversity of behaviours, we should, perhaps, not expect to find universal evidence of social limitation of population densities during the breeding season. Social limitation during the breeding season might, therefore, be expected to occur more frequently in territorial waders nesting in temperate areas (such as Lapwings), rather than high arctic species.

Regulation of wader numbers might also occur on passage and during the winter. Various studies suggest that suitable winter feeding habitat might be limited, that competition for those areas occurs and that sub-dominant birds may be forced to feed in sub-optimal habitats where their feeding success is lower and mortality may be higher (Goss-Custard 1981).

In summary: although there is evidence that at least some wader populations may be regulated on their breeding grounds by the action of density dependent factors, in the absence of further studies it should be treated with caution. The answer to the question, whether waders are regulated, is unlikely to be a simple one since the extent of regulation is likely to depend on species specific extrinsic and intrinsic factors. These may include climate in the breeding and wintering areas, migration pattern and social behaviour during the breeding and non-breeding seasons. Since these all vary widely between species (and populations), it is to be expected that the occurrence and degree of regulation might also vary. This study has shown that it

is possible to investigate and, perhaps, measure density dependent processes in breeding waders and that territoriality may have an important role in the regulation of Lapwing populations. This latter finding may well apply to other temperate zone species which are territorial while breeding, but only further intensive and, more importantly, experimental field work will confirm this. Such studies will be essential if we are to understand fully the factors and processes influencing wader population biology.

Prospects for Lapwings

Given the current agricultural trends toward the intensification of cereal farming and the improvement of marginal land, the long-term prospects for Lapwings breeding on British farmland are not good. The effect on breeding success of the reduction in the acreage of pasture and the intensification of cereal cropping has already resulted in local population reductions and extinctions on arable farmland. Moreover, on rough grazing, where there is, apparently, competition for breeding sites and habitat availability may limit numbers, rapid land-use changes have also occurred, as marginal land has been improved by drainage, re-seeding and fertilisation. This, also, has resulted in local reductions in breeding numbers. The extent of these reductions is not known since British Lapwing populations are not monitored on a regular basis. However, it is known that in many areas of the country (especially the south and east), where once they were common, breeding Lapwings have become scarce or absent altogether.

If these agricultural trends continue, the conservation of the remaining rough grazing birds will assume great importance. This may be the most productive component of the overall British mainland population and, as such, might provide a reservoir for the future re-colonisation of lowland farmland (if, once again, it should become

suitable as a breeding habitat). Because of the conservation implications of further improvement of rough grazing habitats, any future research on the relationships between farming and Lapwing breeding ecology should be focussed on this habitat.

In particular, we need to gather more detailed information on the relationships between habitat structure, breeding density and success. Why are some areas of apparently suitable rough grazing habitat unoccupied? What is the relationship between habitat heterogeneity, i.e grain size, and breeding density and success? How do specific farming activities, e.g grazing intensity, alter the suitability of rough grazing habitats, and how should the habitat be managed to ensure the conservation of the remaining Lapwing populations. At present, the Lapwing is still a relatively common breeding bird in many areas of the country but all of these questions will assume greater importance if, as seems likely, the birds which breed on much of Britains more intensively managed farmland continue to decline.

SUMMARY

1. The breeding ecology of Lapwings in relation to agricultural land-use and habitat was compared in rough grazing and arable study areas in the Midland Valley of Scotland.

2. Birds arrived on their breeding areas in early February. Males preceeded females and territory occupation by the males began soon after first arrival.

3. During the pre-breeding period birds remained in flocks and day-time habitat use and activity was strongly influenced by the lunar cycle. Birds fed mainly in those habitats in which prey (leatherjackets and earthworms) were most plentiful, and in which their feeding success was higher.

4. The choice of nesting habitat was not influenced by food availability in the immediate vicinity of the nest site but by the crypticity of the clutch and incubating adults. On the rough grazing sites birds preferred unimproved land, while on the arable, spring cereals was the preferred habitat. The choice of actual nesting field on the arable site was influenced by the risk of predation and the proximity of suitable feeding habitat for both the adults and chicks (permanent pasture). Thus, birds selected large spring cereal fields distant from trees or hedges (which might conceal predators) but close to permanent pasture fields.

5. The laying season extended from late March until late May. Weather appeared to have little effect on the timing of the start of laying. On the arable site, the season was cut short by crop growth in the cereal fields.

6. In both habitats the modal clutch size was four eggs (78% of clutches) and was unaffected by laying date or clutch number. Disturbance during cultivation was, however, responsible for a greater frequency of smaller clutches early in the season on the arable land.

7. Eggs consisted of 33.1% yolk, 61.3% albumen and 5.6% shell. Whereas the yolk and shell proportions decreased with increasing egg size, the proportion of albumen increased.

8. The incubation period varied between 21 and 28 days (mean = 25.2) and was shorter in clutches laid later in the season. The reduction with laying date was probably due to a behavioural change on the part of the adults.

9. Most variation in egg size was attributable to differences between females and was influenced by clutch number (eggs in replacement clutches on the rough grazing, but not the arable, site were smaller), clutch size (eggs were smaller in smaller clutches), maternal body condition (females in good condition produced larger eggs) and habitat (since females on the arable site fed more successfully, they were in better body condition and laid larger eggs).

10. Breeding success and chick behaviour was heavily influenced by a combination of predation, egg size (and, hence, maternal body condition), weather and land-use:

a) hatching success. Most failure to hatch was due to predation (heaviest on the rough grazing sites). On the arable site hatching success was further reduced by losses during cultivation.

b) brood movements. After hatching chicks moved to improved land (the rough grazing site) or intensively grazed permanent pasture (the arable site) where the vegetation was shorter and food more plentiful. On the arable site this habitat shift was at least partly a response to rapid crop growth in the natal spring cereal fields. In 1986, when crop growth was retarded by adverse weather, chicks remained in the spring cereal fields.

c) chick survival and productivity. Most chick mortality occurred in the first few days after hatching and was influenced by chick movements, the pattern of land-use, egg size and hatchling body

condition, and the effect of weather on crop growth. On the arable land, chick survival during the first two years of the study was poor and determined by the proximity of permanent pasture to which the chicks could move after hatching. In the final year, cold, wet conditions retarded crop growth and the chicks were able to remain in the cereal fields and survived better. Larger, heavier chicks hatched from bigger eggs. These grew faster and survived better than chicks from smaller eggs. Late hatched chicks had poorer survival.

On average, rough grazing females raised 0.8 fledglings per year. The corresponding figure on the arable site was 0.4. Productivity on the arable site was not sufficient to compensate for adult and juvenile mortality and the population appeared to be declining.

11. There was no evidence for any direct density dependent effect on either hatching or fledging success. However, on the rough grazing site, variation in breeding success and the temporal and spatial settlement patterns conformed to the predictions of the ideal despotic model. It is possible, therefore, that territorial behaviour may have a density dependent effect through exclusion of settlers into sub-optimal habitats where their breeding success is low.

12. Chicks probably fed opportunistically, rather than selectively, and their diet comprised mainly Coleoptera, leatherjackets (Tipulidae) and earthworms. Although few in numbers, earthworms, because of their relatively large size, comprised at least half of the prey biomass.

13. The post-hatching pattern of development is adaptive in that the structures with a high early priority, e.g locomotory and feeding apparatus, are comparatively mature at hatching and develop quickly. In contrast, the development of flight capability begins late (after the chicks have reached a suitable feeding area and are feeding efficiently). Growth rates were influenced by hatch date (late-hatched chicks grew more slowly), egg size (chicks from large eggs grew more

quickly) and, hence, maternal body condition, and whether or not the chicks had completed their post-hatching movements.

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